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A PRELIMINARY ENQUIRY INTO THE INFLUENCE OF SOLAR RADIATION ON INSECT ENVIRONMENT

WITH SPECIAL REFERENCE TO THE RELATION BETWEEN PEST EPIDEMICS AND FLUCTUATION IN SOLAR RADIATION

By W. B. R. LAIDLAW, D.Sc.

CONTENTS

PAGE

Foreword 20

Section I. Effects of Solar Radiation on Plant and Animal Life.

A. Physical:

Introductory 20

I. Electromagnetic Spectrum 21

II. Solar Spectrum.

(A) Effects on Atmosphere 21

(B) Physical Properties of Solar Radiation (terrestrial) 21

(C) Biochemical Effects 22

(D) Effects of Water 22

(E) Effects of Atmosphere 23

(F) Effects of Altitude and Season 23

B. Biological:

I. Biological Reactions to Solar Radiation.

(A) Short-wave Radiation 23

(B) Long-wave Radiation 24

II. Variation in Radiation Optima.

(A) In Plants 25

(B) In Animals 26

(C) Ecological Differences in Light-tolerance 26

PAGE

(D) Ecological Zoning according to Radiation Conditions 29
(E) The Radiation-water Link 31
(F) Day and Seasonal Radiation Optima 32

Section II. Fluctuations in Solar Radiation through Sunspots, and their Effect on Life.

I. Definition of Sunspots 34
II. Effects on Weather 35
III. Sunspot Occurrences 35
IV. Sunspot Cycles 35
V. Correlation of Epidemics with Sunspot Fluctuation and with Associated Changes in Radiation 36
VI. Fractional Cycles 39
VII. Climatic Trends 41

Section III. Classification of Pests according to Radiation Optimum Conditions.

I. Pest Defined 43
II. Functional Position of Insects.
(A) Influences on Population Numbers 43
(B) Limiting Influences of Environment. 43
(*a*) Physical Environment 44
(*b*) Edaphic Environment 46
III. Types of Pest.
(A) Full Light-tolerant Types 47
(B) Light-intolerant Types. 47
(*a*) Shade-dwellers 47
(*b*) Light-avoiders. 49
(i) Root-feeders 50
(ii) Food-burrowers 50

Section IV. Epidemics—Control and Prevention.

I. The Operative Factor.
(A) The Operative Factor in Reduction of Insect Epidemics 51
(B) Sequence of Factors in Epidemics 52

PAGE

II. Natural Control in Operation.
(A) Full Light-tolerant Species and Soil-dwellers .. 53
(B) Shade-lovers and Food-burrowers 54

III. Applied Controls, based on the Operative Factor.
Introductory 56
(A) Light-tolerant Types 56
(B) Shade-lovers 58
(C) Light-avoiders 59
(D) Sylvicultural Causes and Prevention of Forest Epidemics.
(*a*) Natural Woodland 60
(*b*) Artificial Woods. 62
(i) Pure Wood, Uneven-aged 62
(ii) Pure, Even-aged Wood 62
(iii) Complete Uniformity of Crop 64
(iv) Sylvicultural Prevention of Epidemics .. 65

Section V. Research Fields.

Introductory 66

I. Construction of Forecasts with Prevention and Control Application.
(*a*) Astronomical 66
(*b*) Physical 66
(*c*) Meteorological 68
(*d*) Botanical 68
(*e*) Biological (Entomological) 70

II. Control by Radiation.
(A) Outline of Future Possibilities 72
(B) General Application of Control Principles .. 74

III. Suggested Lines for Biological Experiment.
Introductory 76
(A) Botanical 78
(B) Entomological 78

Acknowledgements 79
References 80

FOREWORD

The majority of the conclusions here arrived at are the result of deductive reasoning from facts and data with the aid of what knowledge, experience and immediate reference works were at hand. It has been satisfactory that all subsequent work referred to has confirmed, rather than discounted, the arguments and hypotheses set out.

Of these latter references I would mention more particularly, Duggar's masterly compilation—The Biological Effects of Radiation, in two volumes; and Uvarov's Monograph on Insects and Climate in the Trans. Ent. Soc. 1931, much of which I have referred to and quoted from in the text.

For the elements of radiation given at the beginning of the paper I am almost entirely indebted to Duggar's publication.

Since completing the bulk of this paper I have read and made extracts from the same of all biological material that appeared to have a bearing on the matter. These are given as footnotes; and here again it has been a source of satisfaction to find so much confirmation of my often tentative deductions and suggestions, in these accounts of proved experimental work.

No one can be more aware than myself, that much of the suggested research would be difficult and very expensive, much would be impracticable, at least at the present time, and much would involve very long-term work covering many years.

I would conclude with the comment that the idea of solar or astronomical influence being in any way responsible for fluctuation in animal and plant populations or state of health, has met in the recent past with considerable scepticism. I believe it is true to say that such an attitude no longer seriously obtains. Scepticism is a product of the closed mind, for which there is no place in biological research.

If the ideas contained in the following paper should succeed in adding a stimulus to this tremendous field of enquiry, they will have fully achieved their object.

I. EFFECTS OF SOLAR RADIATION ON PLANT AND ANIMAL LIFE

A. Physical

Introductory. This paper constitutes a collective enquiry into the biological responses to solar radiation, and before entering into enquiry and discussion along these lines, it is necessary to review as briefly as possible the elementary facts relating to radiation.

Electromagnetic radiation is radiant energy, emanating from its source in waves (employing the wave theory as an explanatory

basis). These waves vary in size and their properties vary accordingly. Travelling at 186,000 miles per second (in air); their length varies from 6,000 miles from crest to crest, when they vibrate only 30 times per second; to 1/10,000 Å (Å=Angstrom, or one 250 millionth of an inch), vibrating at over 30 quintillion thousand times per second.

I. ELECTROMAGNETIC SPECTRUM. Different wave-length regions have received different names. From the shortest Cosmic, Gamma and X-Rays (.0001Å—1,000A) we come to the terrestrial solar spectrum, ultra-violet, light, infra-red, the remaining long waves being classed under Radio Waves and slow oscillations (10,000,000 Metres).

Measurements. The ultimate unit is the centimetre.

The Micron (μ)=10^{-4}cm.—extreme infra-red.

The Millimicron (m.μ.)=10^{-7}cm. and more frequently the Ångstrom (A or Å=10^{-8}cm., are used with near infra-red, visible and ultra violet).

The symbol λ=wave-length.

II. SOLAR SPECTRUM. Solar radiation, reaching the earth's surface, extends from 2,900 Å (ultra-violet) to 130,000 Å (infra-red).

The different regions of the solar spectrum reaching the earth's surface are as follows:

Ultra-violet (near) ..	2,900—4,000 Å
Violet	4,000—4,700 Å
Blue	4,700—5,000 Å
Green	5,000—5,300 Å
Yellow	5,300—6,000 Å
Orange	6,000—6,500 Å
Red	6,500—7,800 Å
Infra-red (near)	7,800—130,000 Å (or 13 μ)

(A) *Effects on Atmosphere.* The total solar radiation reaching the earth's atmosphere produces through the shorter wave-lengths, chemical changes which increase the ozone and form a layer (ionosphere), impenetrable to the shorter wave-lengths, which are destructive to terrestrial life.

(B) *Physical Properties of Solar Radiation (terrestrial).* Maximum solar energy occurs at 4,700 Å, that is in the blue spectrum. At the earth's surface, 1 - 5% solar energy is ultra-violet (3,000 - 4,000 Å), 41 - 45% is visible light, and 52 - 60% is infra-red.

Beyond 7,800 Å (red), or in infra-red wave-lengths, we are aware of these waves as radiant heat, while above 4,000 Å (violet) in ultra-violet region they produce chemical changes and are hence known as actinic rays. Pigmentation of the skin in sunburn is one of the

best known effects of ultra-violet. These actinic properties extend into the colour spectrum to the blue region, while the heat property of infra-red also extends into the red spectrum.

Light travels slower through water (140,000 miles per sec.) or three-quarters of its speed in air, the blue-green wave-lengths being the most penetrative. Different parts of the spectrum vary greatly in their powers of penetration of fluids and solid matter. Thus, ultra-violet can penetrate air, some types of glass, cellophane, superficial plant cells (in young or thin-walled tissues), animal skin. It has little power of penetrating water, either in mass or in atmospheric vapour, while animal and vegetable oils and waxes are also opaque to it. It is reflected from metallic and probably also from polished surfaces.

Infra-red is much more penetrative than ultra-violet or light, its use in deep therapy is well known, and its penetrative power of solid matter is employed commercially.

When radiation comes into contact with anything, atmospheric, fluid or solid, it is either transmitted, absorbed or reflected. All these are of biological importance, but biological effects are only caused by absorption.

(C) *Biochemical Effects.* The manner in which solar radiation produces changes in the living cell may be summarised as follows: (Duggar Vol. 1 p. 87). If exposure of a living cell to radiation causes any change, it must have received some energy which at least initiated that change. Thus the cell receives a small amount of energy which initiates chemical changes, the much greater energy required to complete these being supplied by the chemical changes in the cell.

Energy can be transferred to the cell by radiation only through interaction of matter and radiation. This interaction of matter and radiation is an atomic phenomenon concerned with ionisation.

The biological action of radiation takes the following sequence:

(a) Ionisation.
(b) Chemical Changes.
(c) Biologi[illegible] Changes.

Further chemical changes may then result from (c).

(D) *Effects of Water.* The rapid increase of absorption of water to wave-lengths shorter than 0.2 μ and to those longer than 2.0 μ (2,000 Å - 20,000 Å), sets a natural limit to the range of wave-lengths to be considered. Thus the range of wave-lengths under consideration represents an interval of relative transparency for water.

The outstanding characteristic of matter with respect to radiation in this region, is that of high selectivity, i.e., rapid changes of absorption with varying wave-lengths. From this selectivity the great variety of effects, both biological and physical, arise.

Water is very transparent to the blue-green wave-lengths, to several hundred metres, but at less than 0.2 μ and more than 2.0 μ (infra-red) even 25 mm. of water become opaque.

(E) *Effects of Atmosphere.* Total solar radiation reaching the earth's surface is comprised of two components: (1) Direct radiation and (2) Sky radiation. Sky radiation is an increase due to "scattering" from the sky. The relative contribution of sky radiation is greater for lower sun, when direct radiation travels a greater air path.

Even a light cloud may reduce the total radiation to one-third of its clear value.

The total energy received per day may fall in December to one-quarter of its summer value. The earth's atmosphere, as affected by altitude or air mass, change in water-vapour and ozone, presence of dust and smoke, all cause great variation in radiation reaching the earth.

With high sun, maximum wave-length intensity per unit wave-length occurs at about 5,000 Å (green). Sky radiation, however, is much stronger in blue and ultra-violet.

(F) *Effects of Altitude and Season.* Increased altitude shows increase in solar radiation intensity owing to atmospheric reduction in density with increased height.

Dust and water vapour absorb strongly in infra-red and long-wave regions.

Intensity is less in summer than winter owing to reduced distance in winter of the earth from the sun. January intensity exceeds July intensity by 7%. The low summer intensities are, however, largely due to increased dust and water vapour, rather than to sun-distance.

The total radiation received at the earth's surface consists of "direct" and "diffuse." The diffuse portion is scattered or diffused by atmospheric gas molecules, dust, etc., in the atmosphere. This total radiation is known as the vertical component of solar radiation, and it is the most important one to vegetation directly, and in part indirectly, to animals and man.

B. Biological

1. Biological Reactions to Solar Radiation

(A) *Short-wave Radiation.* It has been noted that only the longer wave-lengths of ultra-violet penetrate the atmosphere to the earth's surface. The other, shorter waves, cut off by the ionosphere, would be highly toxic to terrestrial life. Even those reaching the earth's surface exert an actinic and stimulating effect on life which can be injurious at times of extra intensity, or as a result of abnormal exposure. Indeed the physiological and ecological precautions

taken by organisms to protect themselves from toxic effects of over-exposure can be said, in a sense, to be well-nigh universal.

With animal life, effect is chiefly on the nervous system. Transmission is effected by the superficial skin layers, reaching the blood stream via the small skin vein capillaries. Organisms mature more quickly, though mere growth may be inhibited. Fertility is increased, while behaviour associated with mating and breeding, such as swarming and migration is probably stimulated at the same time.[1]

With plants, penetration and absorption takes place through the thin-walled epidermal cells of active tissue to the underlying parenchyma, frequently the photosynthetic chlorophyll tissue. Anabolism and metabolism is increased to the attainment of quick maturity and increased seed production. This actinic property extends into the violet-blue wave-lengths.

Short-wave radiations inhibit growth but stimulate development. Insects reaching maturity in abnormally dark conditions produce larger sized adults over a longer period of time.

(B) *Long-wave Radiation.* Infra-red waves are transmitted and absorbed as radiant heat and are on the whole much more penetrative of water and solid matter than ultra-violet.

Respiration is increased by infra-red and with it the catabolic processes associated with this activity, i.e., stored food is broken down and energy released for plant use. These properties of infra-red also extend into the red wave-lengths to some degree.

The penetrative quality of infra-red is medically employed for treatment of deep-seated rheumatic and other complaints.

N.B.—All footnotes given in the second, biological, portion of this Section are condensed abstract notes collected from Duggar, B., 1935, Biological Effects of Radiation; with two exceptions, which are so indicated.

1. *Animal Reactions to Ultra-violet.* Skin and superficial tissues are penetrated by ultra-violet, the degree depending on colour of hair, etc. The pigmentation of the skin so caused forms a screen against further penetration. The ultra-violet and infra-red rays adjacent to the colour spectrum are transmitted, those beyond, in solar radiation, being absorbed. Sub-cutaneous tissue gets only the long wave-lengths 6,000 Å=orange rays. Bees showed maximum stimulating efficiency at 5,550 Å (yellow) and again at 3,650 Å (ultra-violet).

2. *Plant Reaction to Ultra-violet.* Specific wave-lengths produce a specific biological effect.

(a) Ultra-violet radiation has the following *primary effects* on plants. It inhibits growth; it increases transpiration (blue W.L.); it assists chlorophyll formation; it reduces nitrogen and increases carbo-hydrates; it stimulates anthocyanin production (flower and fruit pigmentation and autumn leaf colour—author's note); it increases calcium and phosphorous content, as does higher light intensity; it forms Vitamin D by absorption of ergosterol of U.V.; it destroys other vitamins; like light, it decreases cell surface tension charge.

Infra-red and red wave-lengths are of too low frequency to initiate chemical changes. Hence, the green region of the light spectrum would appear to constitute the dividing line between actinic and radiant heat radiation. Green vegetation can thus absorb, for their particular properties, both the long and short-wave radiations. Floral colour is largely determined by the seasonal and ecological variation in radiation constituents and intensity (chiefly short-wave).

The actinic properties of the violet-blue wave-lengths are greatly intensified during periods of increased ultra-violet intensity, owing to sunspot increase; and it is possible that a similar intensification takes place in the red and infra-red wave-length at some stage of the sunspot period. Evidence exists to date of slight increase in atmospheric temperature in certain regions at such times. (Section II, para. 1.). (See footnotes).

II. Variation in Radiation Optima

(A) *In Plants.* It has been noted that short-wave radiation inhibits growth, while stimulating development. Thus full sunlight is essential for healthy plant activities, including photosynthesis. Chlorophyll absorbs energy from a narrow portion of the deep red region only, but the ultra-violet to blue wave-lengths stimulate other physiological processes. If these short waves are increased in intensity, the plant processes are increased likewise.

(b) *Lethal Action* of short-wave radiation takes the form of vacuolisation (as with all radiation), and finally, coagulation of protein. In nearly all cases non-solar (terrestrial) short-wave radiations are injurious to lethal on live organisms.

(c) It hinders germination, stomata open under all light, but more slowly under red, and not at all under infra-red. It increases xylem and bast formation, along with transpiration.

(d) *Penetration.* The following tissues are *opaque* to ultra-violet: Epidermis *cuticle* is very nearly—Metzner found cuticle opaque to 3,500-4,000 Å; unanimous testimony exists that *polished leaf surface* protects epidermis against ultra-violet; wood and cork are nearly so (Kohler); seed coats are; wax on leaves and fruit opaque to 3,400-3,800 Å; cuticle, epidermis and xylem absorbed strongly at 2,800 Å. The following tissues are *transparent* to ultra-violet: Parenchyma, phloem, cambium; pure chlorophyll is transparent; natural chlorophyll absorption band occurs near middle of ultra-violet at about 3,040 Å.

Long-wave Radiation. Respiration is increased by infra-red. Water absorbs infra-red, which heats soil and air to optimum for plants (and animals—author's note).

Long-wave radiation is transmitted through leaves more than short waves; transmission being highest at red.

Photosynthesis is most active under red and yellow wave-lengths, but does not continue under infra-red; nor do stomata open under the latter.

Leaves may be injured by infra-red if water supply is short, with temperature and humidity high.

This involves an equivalent increase in vascular and root development and activity to supply the quantity of water essential to these processes, which in turn requires an adequately increased transpiration current to meet the increased physiological demands.

The greater, then, the intensity of ultra-violet radiation reaching a plant, the greater will be the transpiration current and, therefore, the greater the water demand. This has an important ecological significance which will be discussed later. It becomes clear, however, that different plants will have a different radiation optimum, and that they adopt ecological and morphological methods, permanent or seasonal, to protect themselves against excessive stimulation by ultra-violet and other solar radiation. (See Footnotes). Valuable work has been done on the stimulation of hormone production by infra-red and radio wave-lengths.

(B) *In Animals.* As solar radiation, with ultra-violet, approaches an optimum for an animal, it responds with increased health, vigour, fertility and rate of development. We know that reduced light and ultra-violet or their complete removal during development produces larger adults, but the rate of development is slower, and health and vigour are reduced. Again it is clear that different animal types, or even species, will have different optima for light and other solar radiations, according to their normal habit and environment. Some species are found to respond negatively to ultra-violet and light, but positively to red or infra-red or darkness, during development, and vice-versa.

Certain insects respond positively to infra-red and negatively to ultra-violet during larval growth (vide Lubbock (1902) on Ants), but this will depend on the larva's normal light conditions.

(C) *Ecological Differences in Light-tolerance.* All insects do not enjoy full sunlight to the same degree. Future investigation may determine a system of grouping, graduated according to optimum solar radiation demand in terms of the optimum wave-length range and intensity for a type or species. This would vary in some cases for larva and adult.

A general idea of such a grouping may be expressed tentatively as follows:

Defoliating larvae feed, for the most part, more or less exposed to full sunlight, and such might be expected to find their optimum radiation zone somewhere in the blue-ultra-violet region. Those in

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Radio waves may affect the nervous system adversely in animals through conduction currents which cause rise in temperature and degeneration of tissue in excess.

Radiation optima. Ultra-violet dwarfing effect on alpine flora led to conclusion that every plant has its own ultra-violet optimum.

Every species of plant has its own light optimum for chlorophyll formation (which varies with age) and also for photosynthesis.

hot regions, where high atmospheric humidity cuts out ultra-violet, probably have an optimum in the red region. Many aphids feed in shaded conditions having a lower short-wave radiation requirement, and might find their optimum to be in the green-yellow region. A third group feed and develop concealed from daylight, such as root-feeders, food-burrowers and night-feeders. The majority of these are removed from the influence of ultra-violet, which cannot penetrate solid matter. Infra-red and the longer wave-lengths are much more penetrative so that such concealed feeders would be expected to have their radiation optimum in the infra-red region.

Supporting Evidence. Considerable research work has been carried out on the reactions of plants and animal life to different wave-lengths in the solar spectrum. The majority of these have been restricted to the colour-spectrum wave-length. The following extracts from this type of work are of significant interest.

1. Uvarov (1931) gives the following accounts of work done on the influence of various parts of the spectrum.

Schoch (1880) experimented with eggs of *Arctia caja* under red, blue and violet glass. Those under violet glass developed more rapidly, consumed twice the amount of food, and completed their development fourteen days sooner than those under red or blue glass. (*A. caja* is a good type of defoliator feeding exposed to sunlight.) Gal (1898) found the same results with silkworms—the violet light favoured growth, weight of cocoon, amount of silk and number of eggs laid. Zhmuidzinovitch (1891) found the quickest silkworm development under blue light, the rate decreasing in the following order—yellow, white, dark violet and green: while Flammarion (1899) found ordinary dispersed light produced more silk per cocoon and more eggs laid, the effect decreasing in the following order—purple-violet, pale green, pale red, orange, dark red, dark green, dark blue, pale blue.

The silkworm variations may perhaps be accounted for by existence of different temperature conditions in the experiments. Being a long domesticated insect, now adapted to artificial conditions, one would expect its actinic light optimum to be lower, also that it might well respond less favourably to increased actinic light.

Uvarov points out that, while larger individuals have been found to result from ultra-violet, this was in large measure due to low associated temperature, giving examples from other experimental work, where blue light, reflected light and darkness, while slowing down growth, also gave larger individuals. Beclard (1858) obtained largest larvae of *Musca carnaria* with violet light, next, in decreasing order of size, came blue, red, yellow, white and green. The result from the neutral green is interesting as suggesting a

deficiency in actinic or radiant heat effects. Experiments by Lord Avebury (1902) on ants proved conclusively, covering nests with different coloured glass, that *developmental* stages were unfavourably affected by ultra-violet rays and either enjoyed red-infra-red rays or enjoyed them as much as they did total darkness.

He proved that the actinic property and not the colour alone was the undesirable factor by superimposing fluids, colourless and transparent to our vision, but opaque to ultra-violet, over the violet glass, when the ants' objection to leaving larvae and pupae under the violet areas of the nest ceased.

It might be possible to infer from his findings what unfortunately he did not show in his experiments, that radiant heat from the infra-red end of the spectrum provided the optimum conditions for larvae and pupae at a certain wave-length intensity. Nor did he come to the conclusion that insects normally developing in full sunlight will react positively to ultra-violet.

Regarding the reaction to infra-red and radiant heat side of the spectrum of insects, Uvarov quotes interesting points from the literature, having a direct and indirect bearing on its influence and effect. Without quoting all his collected evidence in full, it may be sufficient here to state that it is all consistent in showing that insects which normally develop concealed from direct light react unfavourably when exposed to it. Cave-dwelling species cannot stand exposure to full light conditions. Larvae and pupae of *Calliphora*, *Drosophila*, Corn-borer Moth, were killed or their development slowed down by continuous breeding in darkness, thereafter reacting unfavourably to light (*Drosophila*). The reverse was found to hold good—insects naturally living exposed to light reacted unfavourably to darkness.

The only work mentioned by Uvarov relating to experiments with red light is interesting. Light-avoiding larvae of *Tenebrio* were attracted to and became active under red light conditions, while they avoided white light (Imms, 1937, pp. 74-78).

The results of Graham's (1921-1925) work on the results of study of micro-climates in logs infested by insects are also given. The following significant point is reached—that the temperature in a log does not depend on air temperature, since the absorption of *radiant heat* in direct sunlight causes the temperature inside the log to rise to 60° when the air temperature is 40°. Graham gives a tabular statement of distribution in a log of a highly thermophilous (radiant-heat demanding) species (*Chrysobothris dentipes*) and of *Ips pini*, showing that the latter confines itself to half shaded (therefore cooler) parts of the log, the former chiefly where no shade occurred. *Monochamus* in sun-exposed logs develops in one year, compared with three years in shade. Paterson (1930) gives an

account of control of mountain pine beetle by exposure of logs to excessive radiant heat. Imms (1937) gives examples of effect of light on aphides from Marcovitch (1924), Davidson (1929) and Wadley (1931), where the evidence showed that reduction in light stimulates development of the sexual generation while increase of white light stimulates the asexual generation. He noted in conclusion that experiments on differential effects of limited parts of the spectrum have not been followed up recently, but the subject is one which merits critical examination with modern technique.

Bees and moths are known to have an optical colour vision on a higher range than our own. That is to say they are blind to deep red, but optically sensitive to the longest wave ultra-violet. Moths are strongly attracted to a screen transparent to ultra-violet. (Imms, 1937.) Locusts have been noted to swarm co-incident with sunspot minima where (and possibly when) weather conditions are hot and dry. (Swinton, 1883.)

The eggs are laid in the soil and thus removed from the influence of short-wave radiation, though not from temperature, and thus probably infra-red influence.

(D) *Ecological Zoning according to Radiation Conditions.* (See footnotes.) The influence of atmospheric conditions on the range of solar radiations reaching animal and plant life is very considerable and is closely linked up with elevation and ecology generally. As we have seen, ultra-violet radiation has little power of water penetration; so that high atmospheric humidity forms an effective screen.

With increased elevation, atmosphere decreases in density and humidity, while at low elevations humidity is higher; hence, as is well known, ultra-violet intensity is greatest at high alpine elevation.

From the high elevation of a mountain range, we descend through a continually changing sequence of floral and faunistic zones; each zone having perforce its own particular radiation quality. One would naturally expect, therefore, that an alpine flora and fauna would have a higher actinic wave-length tolerance or demand, while that found at sea level had a very much lower optimum, being also adapted to a higher relative proportion of infra-red to red radiation.

Ultra-violet inhibits growth, which is an important contributory factor to the dwarfed form of vegetation in alpine sites; tree types at low elevations being replaced higher up by dwarf forms (cf. *Betula*, *Salix*). Exposure, low humidity and temperature cannot account entirely for this. This has important implications. If we admit that the insect fauna associated with an alpine flora has a different radiation optimum from one indigenous to a lower, more

humid zone where radiation differs both in quality and intensity, we are led to the following hypothesis:

If we remove a plant native to an alpine site down to a low elevation, it receives now less than its optimum radiation to the detriment of its health and vitality. At the same time, insects indigenous to this lower zone are in full health, and certain of them will be automatically attracted to such an introduced plant, whose reduced health and vitality encourages their establishment on it as serious pests.

This position is closely linked up with the plant's transpiration and water requirement and lies at the root of a number of conifer-*Adelges* problems. For example, European Larch is a natural alpine of high light and ultra-violet tolerance and high water requirement. It suffers little or not at all in its native environment from *Adelges*, where its high transpiration current and sap content preclude serious attack. When grown on a site at low elevation where radiation and water requirements are not met and where *Adelges* is indigenous or in a suitable physical environment, its lower transpiration current, sap content and vitality invite *Adelges* infestation.

Experimental work on the zone grouping of trees and plants in their optimum radiation environment would be a means of clearing up many problems relating to serious injury by pests and disease.

Alpine Plants. The ultra-violet dwarfing effect on alpine flora led to the conclusion that every plant has its own ultra-violet optimum.

Every species has its own light optimum for chlorophyll formation, which varies with age, and also for photosynthesis.

Plants in full sun, and particularly alpine, produce more flowers, while alpines brought to low elevation flower less.

The heavily cutinized and often wax-covered epidermis found among alpines diffuses much light, though some is absorbed. In alpine and desert plants transmission may be as low as 15-25%.

High light intensity hinders photosynthesis, while the relation between the rate of photosynthesis and water content is very important.

White iris petals contain filters against ultra-violet radiation. Schanderl and Kaumpfert found 98% transmission through epidermis of shade plants and only 15-25% in desert or alpine plants.

Epidermis containing anthocyanin reduces the short-wave transmission percentage. Presence of hairs, resins or waxes causes radiation scattering which reduces greatly the total transmission, though there is greater absorption of the shorter wave-lengths. The above authors wish to discard the terms of hydrophyte, mesophyte and xerophyte in favour of a classification based on light-relationships.

Comparison of arctic with alpine plants showed arctic to have a thicker mesophyll, a thinner epidermis and cuticle, resembling shade plants.

Plants develop protective measures against excessive radiation, as follows: short stems, thick leaves, reduced leaf surface, increased water-conducting tissue, more rapid transpiration, root development, increased osmotic pressure and xerophytic features.

Weisner notes that tropical or warm site plants need less light than polar or alpine.

(E) *The Radiation-water Link.* That water requirement is directly proportional to ultra-violet tolerance in plants and animal life there can be no doubt. This can be expressed in another form: Water demand is highest where actinic or ultra-violet radiation is most intense, and where the organism is highly receptive to ultra-violet. When organisms are less light-tolerant or demanding, water demand and transpiration current, with sap content, are lower. (See footnotes.)

Typical light-tolerant trees have a large foliage surface, made up either of moderately large leaves (*Populus*) or a large total foliage area (*Quercus*, *Ulmus*).

Such trees are highly ring-porous to cope with their necessarily high transpiration current (*Quercus*, *Castanea*, *Ulmus*, *Juglans*, *Fraxinus*). Larch is the most alpine of European conifers and possesses a higher water demand and water content than any other; and, furthermore, the more alpine the race of Larch, the larger and heavier the foliage and the stouter the twigs become. Like most alpines, Larch becomes active early and "flowers" early, finding abundance of snow water in spring to meet its high transpiration requirements. Later, in summer, it devotes all its energy to food manufacture and storage for the following season and to the early maturing of its young wood against low winter temperature, which the ultra-violet during the drier summer months amply caters for.

It is probable that such sub-alpine trees as Birch, which are diffuse-porous, have met this ultra-violet problem by a reduction in foliage area and a polished leaf surface which reflects radiation, thus reducing the ultra-violet and light stimulus which its less highly developed water-conducting system could not cope with.

Protective devices against extreme radiation stimulus include

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Transpiration and Water. Very high radiation intensity produces excessive transpiration. Arthur and Stewart note the dependence between transpiration and radiation intensity; injury may be caused by excess transpiration or by heat (cf. young conifers). Frost injury to evergreens is due to excessive transpiration. Most of the energy consumption out of total energy received by green plants is in transpiration = 60%.

Transpiration becomes great at very high light intensities, and to protect against excess, plants show modifications such as low stature, small thick leaves and increase in water-conducting tissue.

Plants eliminate most of their excess energy received in both visible and infra-red radiation by evaporation of water. Whether the transpiration stream does more than effect a cooling during life processes, infra-red is of value in maintaining the stream. 60% of total energy received by the plant is consumed in transpiration.

Desert plants do not flourish where radiation and temperature are high, with limited water supply. Thus they reduce leaf surfaces exposed to photosynthesis and transpiration.

Plants produce most only when there is an adequate transpiration stream to supply the leaf area exposed to radiation.

If water supply is short, leaves may be injured by infra-red when temperature and humidity are high.

reduced leaf size, polished reflecting leaf surface, wax secretion, thickened cuticle and epidermis, production of hypodermis, sunk stomata. These all resemble xerophytic adaptation, which in a sense they are, but are primarily connected with radiation conditions.

Insect Water Demand and Radiation. It has already been noted that insects with a low-radiation optimum (i.e. shade-dwellers) and therefore with a lower water or sap requirement, become attracted to a tree growing out of its optimum radiation environment with a reduced vitality and water-content in consequence. In such a case, serious infestation and injury are liable to result, the insect still further aggravating the deficient transpiration. An insect pest attacking a tree indigenous to its radiation environment would obtain little foothold, the tree being in full health and transpiration flow. The pest would be restricted to the lower drying light-starved branches, a very different set of conditions.

Insects indigenous to low elevation or shaded radiation conditions are unlikely to become pests in higher elevations where more intense radiation prevails.

(F) *Day and Seasonal Radiation Optima.* The intensity and quality

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1. *Leaves.* Of the light falling on a leaf, much is reflected, some absorbed and some transmitted. Much solar radiation is reflected from leaves. Reflection is higher in red than blue, and leaves absorb strongly in violet. Maximum reflection occurs with light green (5,500 Å=yellow). Maximum transmission occurs with green and minimum absorption. Maximum absorption occurs with blue. White leaves reflect all wave-lengths uniformly. Dark green leaves reflect less light than pale. Unanimous testimony exists that polished leaves protect the epidermis from ultra-violet. Thick cuticle and wax coating absorbs much light. Guard cells of stomata show reduced permeability with light exposure, i.e. light induces stomatal opening. Cell permeability depends on wave length, being least with red, green, blue and violet; greatest with ultra-violet and white. Reflection of white underside of *P. alba* leaf=50% of incident light.

2. *Chlorophyll Formation.* A few plants produce chlorophyll in the dark (conifers, ferns, moss, algae). In respiration some radiation is emitted as light which may be enough for chlorophyll formation. Chlorophyll is formed chiefly in orange-yellow and also in blue-violet. Every species has different light intensity optimum for chlorophyll formation and this varies with age. Rate of chlorophyll formation is most during the night, least from early morning to noon.

3. *Photosynthesis.* The wave-length limit for photosynthesis varies with species of plant; e.g. for *P. strobus* and *P. excelsa*=7,400-4,500 Å (red-violet). Starch formation occurs between 7,600-330 Å (red - ultra-violet). Very little energy is used in photosynthesis, the rest goes in transpiration and re-radiation. Energy used in photosynthesis=.66; in transpiration=48.39; transmitted by leaf=31.40; lost by thermal radiation=19.55. The quenching of fluorescence of chlorophyll during photosynthesis is accomplished by oxygen, the radiant energy absorbed by chlorophyll being transferred to oxygen; but the chlorophyll may use the energy through reaction with oxygen (=crux of energy release in respiration). In phototropism blue is most effective—10,000 times that of green and 20,000 times of yellow. Violet is half as effective as blue.

of radiation varies throughout the day, and through the course of a season. Seasonal life-histories of insects show that different types are active at different times of the year and at different times of the day and night, thus selecting their particular light and radiation optimum.

With plants, early spring activity is a feature of alpine vegetation, with early flowering and seeding, when water supply is abundant and radiation less intense than later in the season. Flower coloration is largely determined by radiation conditions. Blue, purple and white are prevailing colours with early flowering alpines and to some extent with autumn flowering species, which thus reject the intense actinic short-wave radiation occurring at high elevations, in whole or in part. Flowers in hot to tropical environments where atmospheric conditions prevent short-wave penetration at low elevations, and where water is deficient, are frequently red, thus rejecting the heating long-wave radiations. In temperate zones early flowers tend to be yellow, accepting long- and short-wave stimuli; those appearing

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1. *Flower Coloration.* Red pigment in red seaweeds (Rhodophycaceae) allows absorption of penetrative blue wave-lengths (Weaver and Clements, 1938). Ultra-violet increases flower production, flowers being more sensitive than leaves to short-wave radiation. Ultra-violet to blue wave-lengths increase anthocyanin production, so that flowers are deeper in colour; red wave-lengths are less effective and green not at all. Blue to ultra-violet also colour certain fruits (apples).

Crocus, tulip, iris and hyacinth develop pigment in the dark; while *Brassica*, *Tropaeolum* and *Papaver* develop pigment only in the light. Red pigmentation is reduced in the dark. White iris petals contain filters against ultra-violet (author's note: cf. numerous white-flowered spring alpines).

Alpine meadows contain a greater proportion of brightly coloured flowers (Weaver and Clements, 1938). It is suggested that the lower temperature and higher light intensity in alpine situations favour pigmentation, anthocyanin being developed best at low spring and autumn temperatures.

2. *Long- and Short-day Plants.* Length of day and night are important in plant development. Plants may be divided into: (1) Long-day plants, (2) short-day plants.

The wrong length of day prolongs the vegetative state indefinitely: thus reduced daylight below optimum increases potato tuber crop (long-day plant); therefore plant "seed" from North in district further South. By contrast, increased daylight increases onion crop.

Short-day plants are brought to flowering stage by short-day exposure. Long-day plants are made to flower by long-day exposure or by continuous daylight.

Exposure of short-day plant to excessive light produces giant forms; while exposure of long-day plants to reduced light produces a protracted vegetative stage.

3. *Altitude and Other Influences.* Tropical and sub-tropical plants have a short day (10-14 hours). Arctic and alpine plants have a long day. Desert plants perform all their photosynthesis in the first few morning hours.

Linnaeus notes that polar plants show quick growth and early maturity in continuous daylight which also produces small leaf, much chlorophyll, little mechanical tissue and early flowering.

later tend to pink tones, or red in dry sites, while blue to purple appears latest when ultra-violet and short-wave effects are most intense. Thus, though flower colour attracts insects, the primary determinant cause of specific colour in a species is radiation, according to the degree of protection against, or acceptance and absorption of, different wave-lengths. Various tones of red, pink and crimson are a feature of acid peat and coastal flora, where water supply is either lacking, or in the case of acid peat bog and salt marsh, of too high chemical concentration to be available to the plant. Shade-loving woodland plants are largely white flowered. Floral colour sequence tends, in low or average elevations, from yellow to red and finally blue in midsummer. Spring flowers thus accept heat and actinic radiations, while later flowers protect themselves from heat absorption with red colour, or from short-wave radiation in July-August with blue-purple when actinic radiation is most intense. The daily time of opening, and the length of time open per day has also a radiation significance. Fluorescence and luminescence properties of certain flowers get rid of unwanted solar energy absorbed through the day and may in the latter instance serve to advertise their presence to late flying moths and other insects. These last are all complex and intricate problems rather outside the scope of the present paper.

II. FLUCTUATIONS IN SOLAR RADIATION THROUGH SUNSPOTS, AND THEIR EFFECT ON LIFE

1. Definition of Sunspots.

A detailed explanation of the phenomenon of sunspots falls outside the scope of the present enquiry. It is enough to state here that sunspots are localized centres of inner disturbances in the sun, apparently caused by planetary configurations (those of Venus and the Earth have been noted), which escape to the sun's surface as radiant energy, etc., and greatly increase the ultra-violet or short waves emanating with other solar radiations from the sun.

Sunspots undergo periodic fluctuation, 11.13 years being one of the most clearly defined periods.

Normal radiation from the sun consists of the complete solar spectrum. During periods of sunspot increase, the ultra-violet wave-lengths are known to be increased.

It is also known that during sunspot increase the blue-violet wave-lengths are considerably strengthened; and that wireless radio is disturbed due to solar effects on the ionosphere. It may be that the radio waves now known to emanate from the sun and the other long wave-lengths in infra-red and the red side of the colour spectrum are also intensified. Pettit found differences throughout

the solar spectrum during sunspot fluctuation; most pronounced in the short waves, and scaling down to almost zero in near infra-red.

II. Effects on Weather.

There is considerable evidence to show that sunspot periods exert considerable influence on weather. From a correlated study of the two, it appears that weather follows a sequence of general trends: being hot and dry during minimum intensities, warm and humid approaching and during maximum intensity, and finally cold and dry as intensity falls to near minimum again.

III. Sunspot Occurrences.

The existence of a cyclic occurrence appears to have been discovered by Schwabe in 1843, but about 1900 Schuster (1900) placed the existence of the cycle beyond all doubt, showing the average interval between one maximum and the next to be 11.13 years. MacLagan has noted what is of biological importance, namely, that the periodic curve is not symmetrical. This asymmetric nature of the sunspot cycle curve is of great importance in explaining the apparent irregularity of epidemic occurrence with certain species, which do not respond to the maximum ultra-violet intensity.

Such have epidemic recurrence in fractional cycles and are dealt with in detail on page 40.

MacLagan states, "The intervals between maxima and minima tend to be longer than the succeeding intervals between minima and maxima"; in other words, the ascent to maximum intensity is more rapid, the falling off period more gradual. "Further, the intervals between successive maxima and minima are not constant, varying from 8 to 15 years."

"The increase in solar-spottedness since the minimum of 1933 has been one of the most spectacular ever recorded and the maximum of 1938 is exceptionally high." (Recent records indicate that the subsequent cycle 1950-51 has been even higher.)

IV. Sunspot Cycles.

That these recurrent sunspot cycles are not simple and regular has been amply demonstrated. The existence of double and even quadruple cycles of 22-23 and 44-46 years has been proved by a study of fossil *Sequoias* and lake sediments. Such have been employed in America as a basis for the accurate forecasting of drought and rainfall periods. (Kimble and Bush, 1943.)

The Brückner Cycle of 35 years, discovered by Eduard Brückner, the Viennese climatologist in Europe, was based on temperature records going back to 1730 and rainfall records back to 1815. Since his maxima and minima show 20 to 50 years' variation it is possible that he is dealing with overlaps of the 23-year cycles.

MacLagan gives an account of Abbot's findings regarding the double cycle of 23 years (now regarded as one of the most significant), giving climatic, biological and geological evidence in support of Abbot's double cycle. (Abbot, 1936.)

Some writers claim to have discovered the existence of half and quarter 11-year cycles; while multiple cycles up to 1,701 years, rising in a triple progression series from 7, 21, 63, etc., years, are claimed by Sir Napier Shaw.

This is enough to indicate that until our accumulating knowledge of cycles becomes more clearly defined the matter is a complex one.

Le Danois identifies a major sunspot cycle of 111 years, but is more concerned with lunar periods.

At any rate, it is clear that different U.V. intensity peaks will exert an optimum stimulus on different species of animal and plant; especially when we take into account the variability of associated climate, weather trends and temperature co-incident with the different ultra-violet peaks.

v. Correlation of Epidemics with Sunspot Fluctuation and with Associated Changes in Radiation.

The influence of sunspot variation on the behaviour of animals and plants, causing changes in their rate of development, and a more or less rhythmic fluctuation in population numbers, has been proved by numerous workers in different fields and countries; so that it is now accepted as an established fact by a fully competent body of opinion. Uvarov (1931) states in this connection, "However, the fact that the fluctuations in the numbers of certain insects coincide to some extent with the 11-year sunspot periods can scarcely be disputed." Uvarov gives accounts of corroborative work on this by many scientists. It is not possible to quote the examples he gives in full; but he cites the names of the following authorities: Swinton (1883), Kulagin (1921), Simroth (1908-1909), Schröder (1909), Meyer (1909), Dieroff (1911), Gasow (1925).

Uvarov answers the criticisms of Meissner (1909) and Schuster (1909), who attempted to prove a complete absence of periodicity in insect outbreaks, in the following significant sentence: "He" (Schuster) "concludes that there is no periodicity of the outbreaks, but this criticism is valueless, since it is based on the fallacious assumption that all insects should be expected to respond to climatic fluctuations in the same way."

In the light of statements made elsewhere in the present paper, regarding the different responses of different types of insect to different kinds and intensities of radiation, his reply to Schuster is the more striking.

MacLagan (1940) expresses the same idea in different words when

he states: ". . . moreover, a glance shows that each species has its own particular phase-relationship to the maximum, varying from *Euxoa* at one extreme to Ague at the other; thereby indicating the variety of ecological conditions presented by the environment at different phases in the cycle of solar spottedness. While one would not expect all species to respond in the same way to fluctuations in the number of sunspots, an explanation of this trend towards mass periodicity, in addition to a distinct periodicity in different species, must be sought in some general climatic pulsation, associated with the periodicity of sunspots."

Other authoritatively supported evidence, too long to quote here in full is brought forward by MacLagan. Towards the end of his paper, however, he advances the following proposition, which has a strong bearing upon some of our previous statements regarding the variable properties of light radiation; more particularly in respect of the different wave lengths producing the colour regions of the light spectrum. Having instanced the occurrence of 5-year periodicities in insect outbreaks taking place between the maximum intensity periods, MacLagan goes on to say: "The other tentative explanation is that the epidemics may be associated with little known factors concerning the quantity and quality of solar radiation, especially in relation to the physiological effects of different wave-lengths. Flint and McAlister have definitely shown that in germinating seed plants, the violet-blue light promotes a set of physiological processes quite different from the set which is promoted by orange-red light, and it was shown by Gal, as long ago as 1898, that the growth of silkworms and the number of eggs laid by the resulting adults are greater under violet light than under normal light. It appears, therefore, that different wave-lengths have markedly different effects upon the reproductive and other physiological processes of insects, and recent investigations emphasize the importance of the shorter wave-lengths. Now as already indicated, the researches of Pettit have shown that the epochs of sunspot-maxima are attended by an increase in the energy of the shorter waves, i.e., the blue parts of the solar spectrum are considerably strengthened. The actinic properties of these rays have long been realized although not completely understood, and they may operate either directly upon the organisms or through their food-plants, e.g., by effecting an increased vitamin-content in the latter. There is still much to be discovered regarding the importance of the ultra-violet rays in relation to the all-important vitamins and the controlled functioning of hormones." Regarding this last point, it is now known that infra-red and radio-frequency waves have a stimulating effect on hormone production in plants, some of which are responsible for vitamin presence in the appro-

priate part of the plant system. MacLagan gives instances of periodicity in the case of six species: Mosquitoes (Ague); Antler Moth (*Cerapteryx*); Leather Jacket (Tipulidae); Turnip Beetle (*Phyllotreta*); Diamond-back Moth (*Plutella*); and Cut-worm (*Euxoa*); showing that epidemics of these species all tend to precede sunspot maxima, or, to be more precise, to lie in that 5-year period which commences three years before the peak and finishes one year after it. Eight to ten epidemic occurrences are given for each insect.

He goes on to show how, if epidemics were quite haphazard, having no relationship to sunspots, the average percentage of all epidemics, lying in this 5-year period of the full cycle, would be 45.4%; whereas the actual average percentage for all six species combined is 71.5%—a difference of 26.1%; which is, as he remarks, a highly significant figure. Further, for each of his six examples, the percentage of total epidemics falling in this sunspot maximum period is above the expected average of 45.4%, ranging from 50% in *Euxoa* to 100% in *Tipula*.

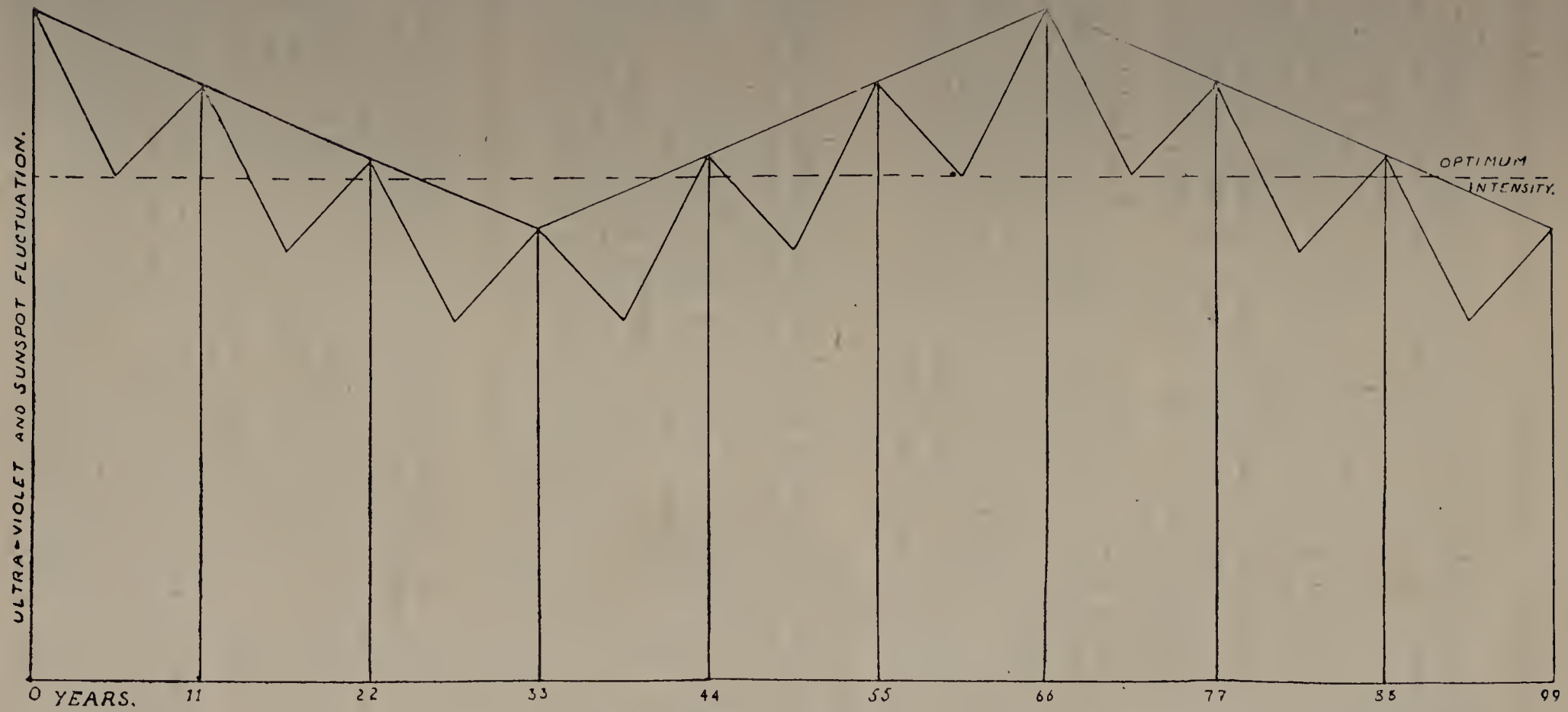
It is to be regretted that MacLagan does not enquire into the lower-frequency, red-infra-red side of the spectrum, but his above remarks provide valuable support for other evidence cited, and for our conclusions regarding the contrasting effects of ultra-violet (with violet and blue) and infra-red (with red and yellow) radiations upon both plant and animal life.

M. Ed. Le Danois (1938), in his important contribution to oceanography and marine biology "L'Atlantique," traces the limits of warm and cold ocean masses. He points out how, by reason of the difference in temperature and salinity, these different water masses do not mix. In his discoveries regarding the existence of a rhythmic expansion and contraction of the warmer superficial water mass centred at the equator, he shows how the expansions towards the arctic and antarctic are astronomically controlled, and identifies a series of periodicities of which the following are the chief: 1 year, 4.6 years, 9.3 years, 18.6 years, which are based on lunar revolution movements every 18.6 years, the others being fractional cycles of this. In addition he notes a centennial period due to displacement in latitude of sunspots, recurring every 111 years, and a lunar revolution period of 93 years.

He concludes this portion of his work by tracing the connection between solar-astronomical periods of 20,700 years, and geological glacial epochs.

The biological reaction to the smaller periods of warm water expansion and contraction shows that plankton and necton populations are limited by these water movements and also the migratory paths and seasons of fish to and from their breeding and feeding grounds, so that fish movements and populations are determined

DIAGRAM 1



DIAGRAMMATIC REPRESENTATION OF 11-YEAR PERIODICITIES AND 66-YEAR MULTICYCLE. (Adapted from Le Danois.)

Broken line indicates optimum U.V. intensity for a pest. Its points of intersection with the sunspot graph explain the irregularity of epidemic recurrence.

entirely by water mass temperatures or by degree of salinity or both.

MacDougall (1939) cites cases of cyclic recurrence of pests. He quotes Middleton (1931) on voles, who found them to have a periodicity of four years and surmised that climatic factors were involved. This does not mean that a plague occurs every four years, but that numbers rise to a maximum and then drop over that period, but in specially favourable circumstances the maximum may reach plague dimensions. MacDougall mentions the possibility of anticipatory preventive measures, such as are practised in America and Europe against the 17-year locust (*Magicicada septemdecim*) and cockchafer.

Mackenzie (1945) gives valuable examples of periodicity from botanical and zoological sources. He instances the well-known occurrence of periodic "full-seed years" in native and exotic trees; also the flowering at regular periods of Bamboo and Agave during the same season over large areas of country. In the zoological field he gives as examples the 4-year period for voles swarming, and 10-year periods for the American rabbit.

VI. Fractional Cycles.

When ultra-violet peak phase provides the optimum conditions for a pest species, epidemic recurrence may be expected at recurrent periods falling at the maximum year for each full cycle.

Many species, however, have their own particular phase-relationship to the maximum; that is, their optimum U.V. phase is below maximum; in these cases epidemics will, therefore, recur over fractional cycles. The successive periods between epidemics will not then be equal, but for any species the periodic *series* over two or more cycles will not vary.

This will become clear by studying the accompanying graph-diagrams 1 and 2. (1).

It becomes clear on scanning diagram 2 that since we are not dealing with a symmetrical curve, where a fractional cycle line intersects the sunspot curve, the distance between the first two intersection points and between points 2 and 3 will be unequal; hence to illustrate the expectancy of fractional cycle epidemics

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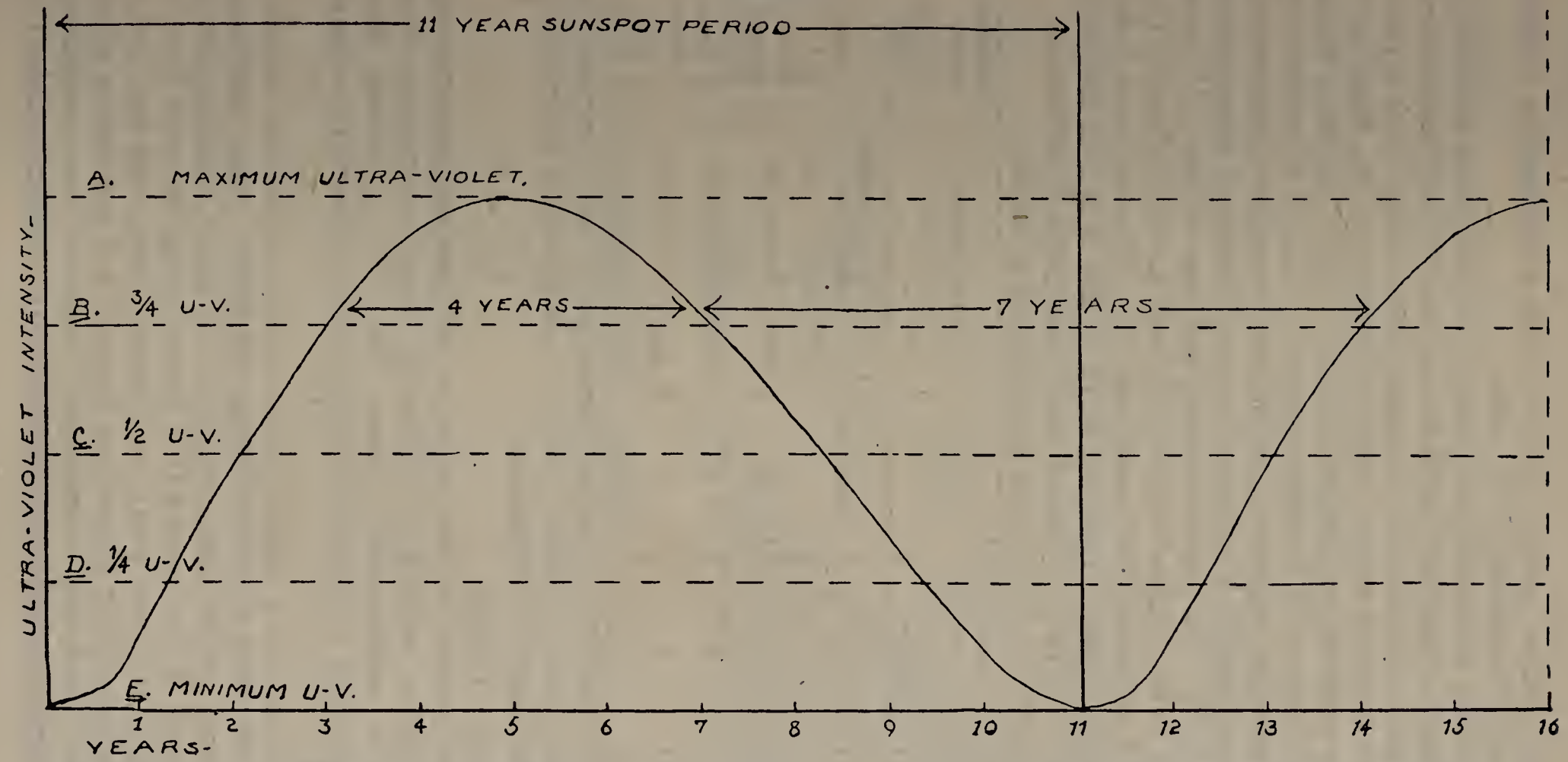
(1) Diagram 2 is based on the assumption of a recurrence of nearly identical maxima for all 11-year periods.
Diagram 1 indicates a multi-cyclic rise and fall over the 11-year periods, so that the maxima are not at constant levels. Though both are hypothetical and quite tentative, Diagram 1 probably shows a closer approximation to the truth, and so offers a better explanation of irregularities in epidemic periods, fractional cycles, and of findings which, in our incomplete state of knowledge, appear contradictory.
Diagram 1 has been drawn subsequent to the writing of this Section.

Diagram 2



Diagrammatic Representation of Sunspot Cycle (11-year) (Ultra-violet vertical axis values only approximate)

Year o represents the U.V. minimum point from which it rises to maximum in year 5—A, B, C, D and E. show (A and E) full maximum and minimum, and (B, C and D) fractional epidemic cycles, where full, ¾, ½, ¼ and minimum ultra-violet forms pest optimum. These are extended to the next U.V. peak to show the difference in period between inter-peak optima and inter-trough optima—see text.

occurring at unequal periods, it is necessary to extend the diagram curve on to the succeeding U.V. peak.

Thus for Case B, when three-quarter U.V. maximum is known to constitute a pest optimum for epidemic conditions, the period between epidemics during the sunspot maximum phase is seen to be 4 years: Epidemic 1 occurring 2 years prior to maximum U.V., Epidemic 2 occurring 2 years subsequent to the U.V. peak. The next period covers the trough or U.V. minimum period, i.e., U.V. continues to drop from epidemic 2 down to its minimum, thereafter rising towards the next maximum till it reaches the pest optimum of three-quarter maximum U.V. The period covering this part of the U.V. phase is now seen to be 7 years between epidemic 2 and epidemic 3 (the latter, which is identical with epidemic 1 is again two years before U.V. maximum point). Cases A, B, C, D and E are, of course, in the nature of our present lack of exact knowledge, hypothetical.

Figures for the five cases may be tabulated as follows:

Hypothetical Cases	*No. epidemics from one U.V. peak to next (incl.)*	*U.V. intensity*	*Years of epidemic occurrence*	*Epidemic periods over 1½ cycles*
Case A	2	Maximum	5th (from sunspot minimum) 16th do. do.	11 years
Case B	3	¾	3rd, 7th, 14th do.	4 years 7 years
Case C	3	½	2nd, 8th, 13th do.	6 years 5 years
Case D	3	¼	1st, 9th, 12th do.	8 years 3 years
Case E	2	Minimum	Minimum year 11	11 years

Thus for Case B the epidemic period series can be expected to run 4 years, 7 years, 4 years, 7 years . . . *ad infinitum*, and similarly with all fractional cycle epidemics.

VII. Climatic Trends.

Reference is made in this section to weather conditions during sunspot periods entering a favourable phase or passing from favourable to unfavourable phases. Diagram 3, derived from MacLagan's paper (1940) shows these trends applied to the sunspot cycle graph.

It shows that during nearly the whole of the ultra-violet increase, up to and extending two years beyond the peak (5 years) conditions are warm and moist—ideal conditions for insect development in nearly all cases. From about ¾ U.V. intensity past the peak down to nearly minimum (years 7-10), conditions become cool and dry, a less favourable climatic phase than the last, and one during which late and early frosts may be expected. These conditions coinciding with a falling off of food supply and population reduction caused by

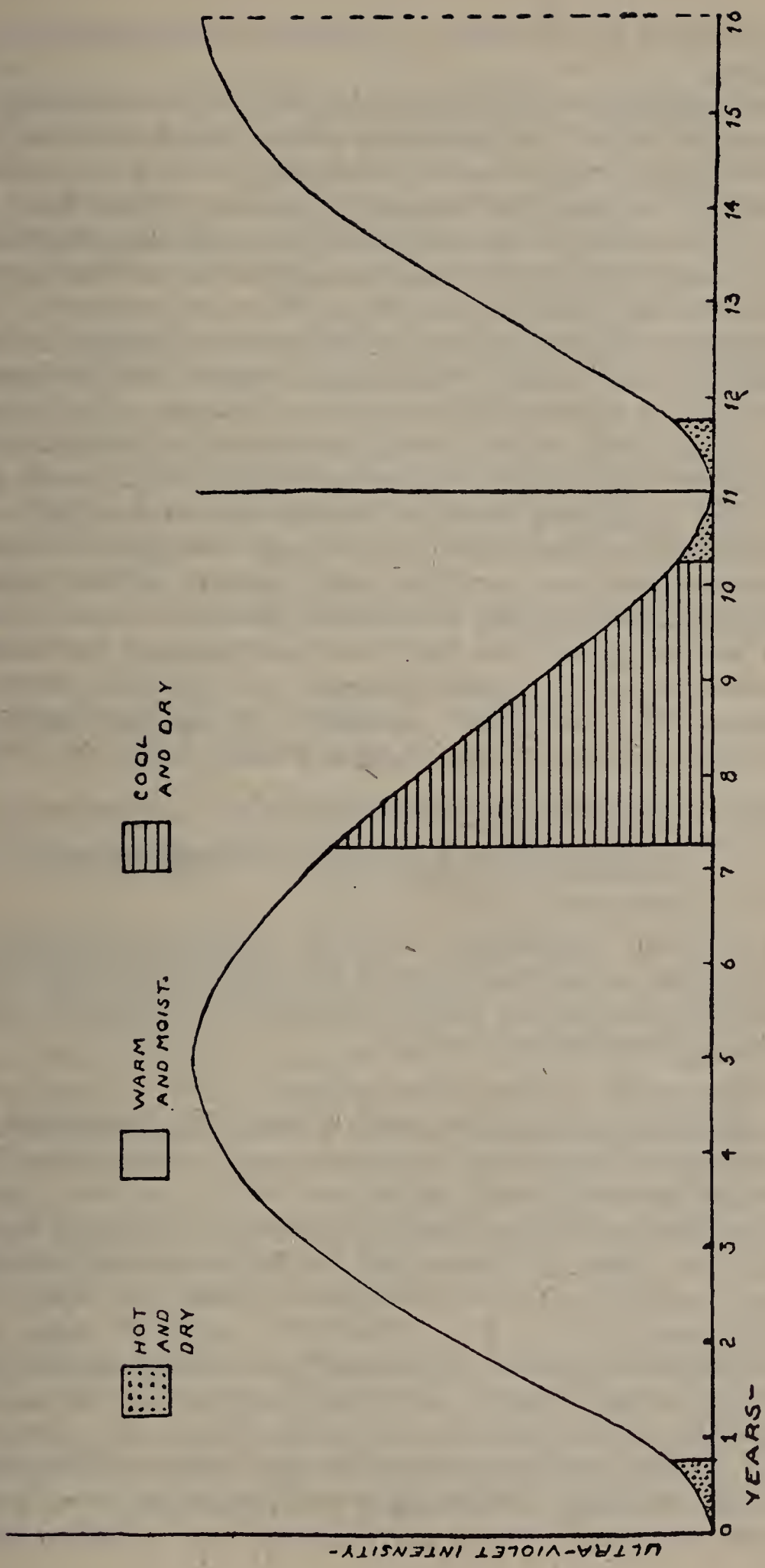

ULTRA-VIOLET INTENSITY-
YEARS-
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
HOT AND DRY
WARM AND MOIST.
COOL AND DRY

DIAGRAM 3

enemies may be calculated to provide the *coup de grâce* to a pest epidemic.

It is probable also that the hot, dry period extending for two seasons over the U.V. minimum period may favour insects which show a negative response to ultra-violet, or which at any rate show a positive response to infra-red radiation. That there is some connection between this weather phase condition and the fact of locusts swarming during sunspot-minima periods has already been referred to in Section I.

Enough evidence has been quoted and cited above to show that epidemics and certain physiological stages in development are influenced by sunspot cycles. Associated climate plays an important part, the warm moist conditions favouring development and population increase up to the sunspot (ultra-violet) peak, while the cold dry conditions inevitably reduce numbers, often suddenly, through late and early frosts and seasonal drought. The manner in which epidemics are correlated with fractions of the 11-year cycle or with fractional cycles, is discussed above.

It would appear also that other astronomical movements and phenomena exert a similar influence of a periodic nature; as for instance the lunar phases described by M. Le Danois. A full appreciation and correlation of these periodic influences is called for.

III. CLASSIFICATION OF PESTS ACCORDING TO RADIATION OPTIMUM CONDITIONS

1. Pest Defined.

A pest may be defined as a species which has, for some cause or combination of causes, increased to sufficient proportions to cause appreciable damage to plants, animals or commodities cultivated, stored or manufactured by man.

2. Functional Position of Insects.

A natural environment contains a mixed flora and fauna (in their broadest sense) forming a vast interacting, interdependent complex in which insects play their part.

(A) *Influences on Population Numbers.* The numbers of a particular species are primarily determined by the presence of a stimulus or stimuli exerted upon or withdrawn from that species in its environment.

Variation in numbers is effected by a change in the quality or intensity of the stimulus (or stimuli) and in one or more of the interacting factors present in the environment.

(B) *Limiting Influences of Environment.* The controlling influences limiting, reducing or increasing the population of a species are present continually in its surroundings; any variation in any of

these will automatically result in a rise or fall tendency in population.

This constitutes the basic key to the principles of applied control.

By enumerating the main factors in the environment of a pest, as completely as possible, we arrive at a stage where it becomes possible to decide which of them can most readily be increased or decreased by human agency, to the detriment of the pest.

Only by deta led investigation of the basic factors underlying epidemic outbreaks, and a full appreciation of their influence, can the cause of epidemic outbreaks be assessed, and the initiation of any form of applied control be effective. For the mechanism of the complex is far too involved to expect an epidemic to be eliminated by using sprays or indiscriminate toxins, or by the breeding and releasing of one species to kill out another. The underlying dynamics are largely physical, and influence pest and enemy alike, so that such elementary methods as the above only touch the fringe of the problem.

The main factors in the environment of a species may be grouped as follows:

(*a*) *Physical Environment*	Solar radiation. Air. Water.
(*b*) *Biological Environment*	Associated flora and fauna—of which we are at present only concerned with: *Edaphic Environment*, i.e. Food Supply and Enemies.

(*a*) *Physical Environment.* We have already noted in the case of plants the close inter-relationship between radiation and water; also the evidence showing that climate is greatly influenced by variations in solar radiation. This is equally true in the case of animal life, including insects. Their water supply is here often indirectly influenced through the insects' food, when phytophagous; but externally, radiation still exerts its controlling influence on atmospheric temperature and humidity. All insects seek out, and are limited by, their optimum environment. Within this optimum, epidemic outbreak is recurrent with certain species. But this physical optimum should be considered not as a point, but as a band or range between a maximum and minimum. Thus an optimum temperature for a certain species is considered not as, say, 65° F., but as lying within a range of, say, 55° F.-75° F. Actual survival range is greater on either side, say 35° F.-95° F. The same principles hold good for humidity and radiation conditions. Thus a certain range or degree of ultra-violet stimulates, and excess above that injures or kills.

(*b*) *Edaphic Environment.* In making enquiry into the edaphic environment of insects, the line at present taken will be to show how radiation optimum dictates the choice of environment and feeding site and how this varies with families, genera and even species. Solar radiation reaching live organisms in a given environment, and the water requirement of these organisms, are directly proportional. Radiation is the precedent factor in the biological sequence. The following corollary is thus suggested—that when a live organism is in its radiation optimum environment, its water supply will also *ipso facto* be at the optimum. Attention will be confined to pests, i.e. forms which are subject to periodic epidemic increase, and cause destruction to vegetation, etc., in consequence.

III. Types of Pests.

Pests, from this aspect, fall into two main types:

(A) *Light-tolerant:* feed exposed to light on fresh food material.

(B) *Light-intolerant:* feed concealed in shade, underground or burrowing inside their food material, the latter in varying degree of sickness or decay.

It will again become apparent how greatly interdependent light exposure and water requirement are in food material.

With light-tolerant types, which feed on healthy vegetation (or food material), the food factor is therefore virtually unlimited, and in this sense, a non-variable factor. It thus exerts no influence on population rise and fall which is primarily controlled by physical factors and hence ultimately by variation in radiation constituents.

With light-intolerant types, physical factors play a less direct part, since these types live and feed largely cut off from direct contact with climatic and radiation influences.

It will be seen that the more advanced saprophytism becomes (i.e. the greater the degree of sickness or decay required in the food plant) the less are population numbers affected by radiation and their dependent physical factors; and also the less becomes the water requirement of the pest. Further, the greater becomes the interdependence between food supply and population rise or fall.

Thus in contrast to the light-tolerant types, food is the main factor and the variable one in respect of the variation in health of the host plant.

On these foundations, a classification of insect types according to their light-tolerance can be sketched out as follows. (Note that this may be completely different for a species in larval and adult instars.) Some insects do most of their real feeding during larval instars—Lepidoptera; others feed on right up to and during maturity—Orthoptera, Aphids, Chafers.

It should be noted that it is those feeding in full light conditions

at whatever stage of their life history, which become subject to epidemic periodic outbreaks.

Thus caterpillars feeding exposed are so subject, though the adult moth, butterfly or sawfly feed little or not at all on solid material. Aphids feed in the same environment in all stages and so are continually subject to this epidemic tendency. Chafers, though soil-dwelling root-feeders as larvae, feed voraciously on foliage as adults and are notable for their periodic epidemics. Thus it is the degree of light exposure *during feeding periods* which is the significant point in relation to periodic epidemic outbreak. That is to say: (1) Insects whose feeding stages (irrespective of instar) are exposed to sunlight (and full radiation influence) are liable to epidemic appearance at more or less regular intervals. (2) Insects which perform their feeding concealed from light and radiation influence are not liable to periodic epidemic outbreak.

(A) *Full Light-tolerant Types.* In their larval instars with some, and during their feeding period generally, these types feed fully exposed to light. Such types are also positively responsive to ultra-violet, as has been proved from certain examples. Defoliating larvae of Lepidoptera and a few sawflies, locusts and other grasshoppers, chafers and other beetles, with certain aphids, are examples of this group. These feed for preference on fresh, young, healthy vegetation in full sap condition and thus commonly, where trees are concerned, towards the top of the outer branch shoots where transpiration is highest. Thus to meet this high radiation stimulus their equivalent high water-demand is fully catered for.

Such are therefore highly responsive to periodic fluctuations in ultra-violet intensity through increase or decrease in sunspots, and show a recurrent epidemic tendency at fairly regular intervals. The length of epidemic recurrence period is liable to vary with group or species. Examples for which this periodicity is well established include locusts, Nun moth, Antler moth, Cockchafer and Cicadas.

(B) *Light-intolerant Types.* Commencing with types which avoid direct sunlight, a graduation of light-tolerant forms exists down to those which pass their early stages completely cut off from light waves if not from other radiation. It will be found simpler to divide these into two groups—shade-dwellers and light-avoiders.

(*a*) *Shade-dwellers.* This type, preferring a greater or less degree of shade from direct sunlight, has a lower light and ultra-violet optimum than the last. Many of these react negatively to white light and to ultra-violet, most particularly in their larval stages. Ant larvae and pupae have been shown to so react to both by Lubbock.

Common examples of this type are to be found among *Aphididae*, *Adelges*.

Aphids constitute an extremely interesting group from this

aspect, in that a complete series of gradations is to be found, from those living under minimum shade conditions (e.g. rose aphids), through deep shade lovers to gall-dwellers and underground root-feeders. Even the most light-tolerant species, however, will be found most congregated on the shady side of plant stems, or on the undersides of leaves and shoots.

Here we can trace the development of the pathological food condition required by aphids affecting the host plant in an increasing degree of response reaction.

In simple cases, the plant responds to the irritation set up by the feeding aphid by a mechanical curling up of the leaf surface, which protects the host from direct light. In more advanced cases, abnormal tissue development occurs at the point of irritation to produce a "gall," this isolating tissue growth more or less completely closing round the aphid and cutting it off completely from light.

In another simple case, very frequently the lower, shaded and therefore weaker, light-starved leaves and branches are selected and here a first stage in pathological development of food material appears (with very significant subsequent implications). These shade-seeking aphids feed on branches which, through light starvation and consequent by-passing of the main transpiration current, which is chiefly to the mid to upper crown of the tree, are sickly and beginning to die off. Such branches are becoming increasingly sap-deficient; but to the aphid with its reduced light exposure, water demand is accordingly less, and thus sap-deficient branches are in an optimum condition for the aphid. There seems to be enough evidence accumulated to show that these shade-lovers are more protein- than sugar-demanding, so that a high sap content, rich in sugar would not be desirable. (See Chrystal, 1925.)

The further implications of this have a very important biological, cultural significance.

In the normal succession of growth of a healthy tree, the presence of such an aphid guest is of little consequence, the aphids only inhabiting those lower portions whose function is nearly completed. In fact, they hasten the drying-up and death of the lower twigs and foliage; their function being thus essentially beneficial. This dying foliage is being constantly replaced by vigorous young shoots higher up where sap current and transpiration are high.

But when a tree's entire water or sap content drops below the healthy optimum to a sickness level which comes into the aphid optimum, trouble of an epidemic nature may be expected. The ways in which this may happen are diverse.

The most important case, and the most frequently overlooked or ignored, is where a tree or plant is native to an environment having a high ultra-violet reception, and is thus highly light-tolerant and

equally highly water-demanding. Plants endemic to the clear atmosphere of alpine situations are largely of this kind.

Introduction of such a species to low elevations where higher humidity reduces light and ultra-violet conditions below its normal optimum, causes an automatic reduction in transpiration through reduced actinic stimulus. Where this condition is combined with insufficient soil water the position is further aggravated and here *all* portions of the plant are brought into a reduced sap condition acceptable to the food requirements of aphids or their allies endemic to this low elevation zone.

In this way the introduction of plant species far out of their light-optimum lays them open to epidemic attack by insects of this type. These insects are responsive to the stimulus of periodic ultra-violet fluctuation, so that epidemics will show a recurrent tendency which may and often do prove serious on such trees.

Climographic study of plant requirements in respect of ultra-violet and/or sunlight, and water (seasonal or general), prior to introduction, could eliminate the danger where large-scale planting is contemplated.

The more light-tolerant the aphid, the less reduced in health will the plant attacked have to be; the more shade-loving, the more sickly condition will the host plant have to reach.

Other causes of sap-reduction to an insect optimum are the more natural and less avoidable ones of drought, and, with trees, wind-blow or fire damage. These may coincide with periodic epidemic optimum physical conditions of potential insect pests, with serious consequences to the crop.

Aphids will attack tomato plants whose growth has been checked by inadequate watering and when this water deficiency is corrected and the plants recover and grow ahead, the aphids leave them.

(*b*) *Light-avoiders*. This type feeds and develops cut off from light, if not entirely from other radiation influences.

Their ultra-violet and actinic radiation requirements are slight or nil, but in some instances (sub-surface feeders such as bark beetles) they may be within the range of influence of penetrative radiations such as infra-red.

Cyclic epidemic recurrence through sunspot periodicity cannot be discounted here since such types will always be indirectly affected by resultant climate and temperature, and by the response of the host plants.

Indeed, this has been shown to be the case by MacLagan in the case of cutworms and leatherjackets. Their soil-surface or near-surface activities bring them at certain seasons or periods inside the range of direct radiation influence during their larval feeding stages. MacLagan found that *Tipula* showed a closer, more consistent

correlation with sunspot periodicity than any other species instanced by him.

They are conveniently subdivided into root-feeders and food-burrowers.

(i) *Root-feeders.* Soil-dwelling insects live in the surface layers of soil, usually not below the top four inches of soil. During dormant seasons in winter, when severe frosts occur, they will descend to twice that depth in Britain, but seldom more.

Being thus in direct contact with the prevailing atmosphere during their active feeding times, and also within the range of certain radiations, at times even including light, they are responsive to periodic fluctuation through sunspot increase and decrease.

How much they are directly affected by ultra-violet and other radiation influence has not yet been fully ascertained. MacLagan's finding in relation to *Tipula* suggest strongly that they are subject to a more direct constant influence than fluctuating weather conditions which go with sunspot periodicity. Accompanying weather trends are often more localized and tendentious than definite in their sequential phases.

Locusts lay their eggs in the surface layers of soil, where radiant heat at the infra-red zone can penetrate. Swarming has been noted for certain species to occur during sunspot minima.

Chafers, whose larvae are root-feeders for a number of seasons, varying with seasonal "temperature" and with species, have already been referred to. Active feeders as adults on foliage in full sunlight, they are then at both stages, and particularly as adults, subject to radiation influence and have long been known to appear in epidemic numbers at regular periods; some species at 11-year intervals, others at less.

Leatherjackets (*Tipula spp.*) and cutworms especially feed at or actually on the soil surface and hence come within the range of radiation influence.

Root-feeding insects, such as wireworms and aphids also fall into this group.

The indirect influence of periodicity in ultra-violet and accompanying weather trends on the host plants of this type of insect, must also be taken into account.

To what extent if at all any of these root-feeders are influenced in their choice of host plant, by its state of health consequent on seasonal drought, unsuitable site, or soil conditions, is, I believe, not at present known. It is possible, however, that some species may be found to show a preference for plants which for some reason or another are not in full health or, in consequence, deficient in sap or water content.

(ii) *Food-burrowers.* This type lives, at least during larval develop-

ment, inside and surrounded by food material. The depth to which they burrow away from the surface varies with family, genus and sometimes with species.

As previously indicated, there is considerable evidence to show that the greater the pathological change required in their food, the less becomes their light and water requirement and the longer their development period to maturity. Thus with such insects as bark beetles (Scolytidae) and larvae of lepidopterous shoot-borers, which feed just below the surface tissues in the phloem and cambium, they are still within range of direct radiation influence. Such feed on host trees, in the case of some species, but little reduced in health and with only a slight reduction in sap flow and transpiration.

Other types such as Longicornia spp. and Siricidae burrow deep into the wood, and prefer dying, dead or even decaying timber which is drying out, or has already dried out. Once again the connection between exposure to light and water requirement is evident; the requirement for one being directly proportional to the other.

It is likely that such types, at any rate the near-surface feeders, will be found to be affected to a varying degree by penetrative long-wave radiations, including infra-red.

The principle has been applied in U.S.A. for the control of bark beetle and other timber beetles, by exposing logs to radiant heat; where it was found that different species had a different optimum exposure for toxic effect.

If these types can be shown to give a response to sunspot periodicity, as is possible at least with the more superficial feeders, it seems most probable that the influence reaches them, either directly by penetrative radiations, through the superficial host plant tissues; or indirectly by radiation influence on their host plant and also by accompanying weather trends.

IV. EPIDEMICS—CONTROL AND PREVENTION

1. The Operative Factor.

(A) *The Operative Factor in Reduction of Insect Epidemics.* The sequence of factors, which leads up to and succeeds any insect epidemic, is the same for all types.

Single factors may vary in intensity or in directness of influence on the epidemic, according to the type of pest involved. For each case, study of the factors in the sequence will reveal which of them can, in practice, be modified or developed.

If the only factor which can be so employed is *antecedent* to the epidemic in the full sequence (i.e. if it appears before and therefore provides a stimulus to the epidemic), *reduction* or *removal* of it will prevent or eliminate epidemic outbreak. Thus with insects which feed on dying trees, such as certain beetles, prevention of an

excessive number of such dying trees occurring, and the prompt removal of any, after, say, fire or wind-blow, will obviate epidemic outbreak. "Food" is here seen to be an antecedent factor in the sequence, and is the "operative factor" in such cases.

If the "operative factor" occurs *subsequent* to epidemic outbreak in the sequence, *stimulation* or *increase* of that factor will reduce or eliminate the epidemic *after* it has occurred. Thus, with defoliating insects which feed on fresh foliage, the antecedent factors, food (healthy trees) and climate, are non-alterables; so that in this case we find the only operative factor is one which occurs *subsequent* to epidemic development—namely "pest enemies." Stimulation or increase of this factor may materially assist in reducing the epidemic *after* it has developed.

Applying these principles to our previous classification of pests, according to their degree of light-tolerance, the analysis of each case and the approach to its solution becomes simple, since on this basis we can readily determine whether prevention or cure is the line to adopt.

(B) *Sequence of Factors in Epidemics.* The sequence of factors containing an epidemic may be tabulated as follows:

Antecedent Factors:

1. Solar radiation, with sunspot intensity, reaches optimum for pest.

   (Note—It is pointed out in Section II, quoting MacLagan, that each species has its optimum phase-relationship to maximum sunspot intensity, which is closely correlated to the optimum phase for the host plant. For one case, therefore, "optimum" may coincide with ultra-violet peak, in others it may lie in the "trough," or again at some point between the two.)

2. Climatic conditions enter favourable phase.
3. Pest food supply present in abundance.
4. Pest population rises to epidemic proportions.

Subsequent Factors:

5. Pest enemies increase under optimum radiation, food and climatic stimulus.
6. Solar radiation with co-incident climate pass beyond optimum phase.
7. Pest epidemic reduced:
   (1) By enemies.
   (2) By diminution of food supply.
   (3) By radiation and associated climate.
8. Pest epidemic eliminated.

The action of solar radiation on vegetation and the plant's reaction thereto is extremely complex. It is highly probable that the stimulus to pest and host is complementary.

1. Thus highly light-tolerant insects are stimulated by maximum solar ultra-violet phase, which at the same time stimulates accelerated metabolism in the indigenous (or fully acclimatized) food plant; resulting in an optimum vigour and consequently in a high sugar content, which are co-incident with high transpiration and full sap condition in the plant.

All these conditions in the plant fulfil the optimum requirements of defoliating insects, so that radiation stimulus to host plant and pest appear to be complementary.

2. Where minimum ultra-violet phase is the optimum for a light-intolerant pest, catabolic processes (always more active in a host plant in a state of reduced vigour, ill-health or disease), under red or infra-red stimulus, suffer a minimum interference through ultra-violet during its minimum phase.

Here again, the radiation influence on host plant and pest are complementary. The host plant being in a condition of low vigour, transpiration and sap content, provides optimum food material for light-intolerant insects.

3. A third contingency should be noted—the intermediate perhaps. Where high ultra-violet stimulus operates unfavourably on a plant out of its optimum environment high transpiration demands are made by the plant, which either immediately or at an early stage cannot be met. Water loss becomes excessive, demand exceeding supply, water and sap content fall, and in its unsuccessful attempt to recover full health, catabolic processes are increased, bringing the plant and pest into conditions comparable to the second case.

As a tentative interpretation of the essential pest food requirements in these three cases; it seems likely that high sugar content is an essential constituent with Case 1—light-tolerant insects; high protein content being essential to insects associated with Cases 2 and 3.

Some evidence in support of this occurs in contemporary literature. (See Chrystal, 1925).

II. Natural Control in Operation.

With all types of pest, it is clear that if food supply is insufficient, widespread epidemics cannot occur. Outward favourable physical conditions may stimulate the tendency to swarming, with, perhaps, small localized response, and harmful effects where the host plants occur; but lacking widespread distribution of the host plant, or if the host plant is not in a suitable condition to constitute a breeding ground, nothing in the nature of an epidemic will result.

(A) *Full Light-tolerant Species and Soil-dwellers.* Where light-tolerant pests and such concealed pests as also feed on fresh food

are concerned, when food is unlimited and, in this sense, a non-variable quantity, epidemics may be expected to recur at regular intervals under radiation stimulus and the resultant favourable climatic conditions. Note that the stimulus will recur quite regularly but the weather conditions, which only obey a trend, may vary locally from year to year, or from cycle to cycle, and thus large universal epidemics need not occur unless local physical factors coincide favourably during full sunspot intensity.

Given such a combination of factors favouring increase, such pests will increase and the conditions favouring them will also favour increase of their natural enemies. Note once again as with pest, so with parasite, unlimited or abundant food is the pre-requisite for rise in numbers, hence the known fact that parasite and predator increase always follows that of the host.

These enemies will of themselves considerably reduce pest numbers; but by the time this is happening a change has occurred in the physical environment.

First the ultra-violet stimulus to development and reproduction has passed its optimum and is becoming steadily less favourable: this also brings about a change in the *trend* of weather conditions from more favourable to more unfavourable—such cold dry conditions, for example, as appear towards the end of a full 11-year cycle are conducive to late spring frosts, which virtually killed the *Adelges* outbreak on Larch, in the spring of 1945. Indeed such fortunate "accidents," local or widespread, may occur at critical stages of pest development in any season.

Changes in weather trends, combined with the regular withdrawal of the ultra-violet stimulus are the more natural and consistent cause of epidemic reduction, of which, enemy increase and attack are only a secondary accompaniment. Indeed it is extremely doubtful whether parasites and other enemies ever eliminate epidemics any more than any organism dependent on another in the biological complex ever eliminates its host. As a matter of biological fact, the whole mechanism of the biological complex operates against such an occurrence. It is the sequence of physical events, with its attendant climatic conditions, which stimulates, first pest, then enemy, and eventually reduces both to their minimum population state in the natural course of the epidemic phase.

This sequence of events applies to such insects as feed fully exposed to sunlight on fresh food, such as defoliating larvae—lepidopterous and sawfly—and to concealed root-feeders such as chafer larvae, wireworm, leatherjacket and perhaps certain sun-loving aphids. (It seems probable that the penetrating infra-red rays have a considerable influence on root-feeders.)

(B) *Shade-lovers and Food-burrowers.* With shade-lovers and

food-burrowers, we have the same sequence of ultra-violet and weather trend variation. These physical factors have a more direct influence on the shade-lovers than the food-burrowers; but both types have in common one important condition: that is the uncertainty of sufficient suitable food material.

Shade-lovers prefer their food in reduced sap condition and thus in reduced health. With trees this will often consist of localization to more suppressed, light-starved branches; though equivalent sap conditions may result from drought, fire or frost damage on entire trees; with, in addition, trees planted out of their optimum environment. Apart from accidental occurrences such as these, it is clear that forest management will largely determine the available food supply. Aphids and *Adelges* are typical representatives of this type of pest. Pest enemies may increase, but here pest increase is limited beforehand by that much more conditional variable, the antecedent factor, food.

With food-burrowers, control sequence is much the same as the last. Direct effect of light is removed, but weather trends still exert an influence in part directly through humidity and temperature, as well as indirectly through their effect on the host plant when this is alive.

Here the condition of the food material varies from sickly and so in reduced sap condition (bark beetles and some weevils), to dying or dead (some bark beetles, Longicorns, Siricidae), or to actually decaying or decayed (some Longicorns and Siricidae).

Note that energy sources are balanced through the whole range of feeding habit. The higher the host metabolism, the greater the pest's light-tolerance and water demand. The greater the host catabolism the less the light-tolerance and water demand of the pest. Life history periods, as is understandable, are commonly much longer in this latter instance. This pathological development of food condition is again determined by forest management and policy: and without such increase of food supply, no epidemics can arise. In a healthy wood, this sick or dead material bears a constant proportion to the whole wood; but artificial conditions of sylviculture, drought, fire damage, frost or clear fellings, inevitable under monoculture over large areas, may again create an abnormal increase in sick or dead trees.

When this coincides with favourable physical condition factors, "pests" will increase as will their enemies subsequently; returning to normal numbers in due course when food material becomes used up or past edible condition, depending on the feeding-type of pest and (again) finally and inevitably when climate and ultra-violet pass from the optimum to the unfavourable phase.

Note again that the more advanced the required state of sickness

or decay of food, the less is the light-tolerance of the pest, the drier the food material and consequently the less also the pest's water demand. Insects feeding on most decayed and dry material are also furthest removed from the influence of light and solar radiation generally. Thus is again exemplified the close inter-relationship between solar radiation and water requirement.

Examples of these insects are as follows:

1. Reduced sap condition: Twig- and shoot-lovers (chiefly Microlepidoptera). Aphids (some spp.). *Adelges* gall-dwellers. Bark beetles—certain spp., notably *Ips typographus*.

2. Sickly to dying condition: Most bark beetles, pine weevils and other weevils. Longicornia spp.—*Rhagium* sp. *Asemum*, etc. *Sirex* larvae.

3. Dying to dead condition: Longicornia spp. *Sirex*.

4. Dead to decayed condition: Certain Longicornia. Clavicornia spp. (Mycetophagidae, etc.). Staphylinidae spp. Myriapoda, etc.

III. Applied Controls based on the Operative Factor.

Introductory. When we come to consider the possibilities of applied control as a means of reducing pest outbreaks, we have now come to appreciate the underlying principles, stated above, and here repeated.

1. Pests can only be reduced by a decrease in one of the *antecedent* factors in the biological sequence; or by an *increase* in one of the *subsequent* factors.

2. Such a controlling factor must be variable and capable of alteration by artificial means.

3. Pest epidemics can only be *prevented or eliminated* through the *antecedent* factors in the natural sequence.

4. Pests may be *reduced* from epidemic numbers through the subsequent factors.

(A) *Light-tolerant Types*. Example 1: If pine sawfly is a local pest on healthy pine, it *could* be prevented from occurring in that locality by reduction or elimination of its food supply, i.e. by clear felling and ceasing to plant pine. This is obviously seldom a practicable proposition.

Example 2: If bark beetles become a local pest, requiring their trees in a sickly condition for food, it becomes a practicable and desirable proposition to *reduce* sickly trees, or to ensure by wise planting, the good health of a wood, thus *preventing* disproportionate increase of such insects.

(With pine sawfly, the food supply is not a variable, or capable of reduction in any practical sense, but with bark beetles it is so in a highly desirable sense, and to treat their food as the variable

quantity, which it is naturally, is the sound approach to prevention of epidemics.)

Example 3: Pine sawfly is a local pest on healthy pine. It is not intended to interfere with the quantity of pine. The next variant and controlling factor here is "enemies." Thus such pests can only be *reduced* after epidemic occurrence (not prevented) by an artificial increase of the enemy factor—or by such artificial substitutes for enemies as trapping or insecticides. (One must not entirely discount the potentialities of artificial control as a precautionary measure taken prior to epidemic occurrence, but it should be borne in mind that the physical stimuli are present at the same time for the pest; and are very likely not at their optimum for enemies.)

Bearing these points in mind, let us consider briefly the possibilities of applied control in relation to our different groups of pests.

Control of Light-tolerant Pests. These feed on fresh, healthy food material. In this case, as stated above, the only line of approach is that of bringing about an increase of the subsequent factor—enemies—or the introduction of a substitute for enemies, viz. traps or chemical methods.

Pest Enemies. Much good may be done by a judicial leaving alone where the biological complex is concerned—for it to work out its own salvation—which it does more often than many give it credit for. The more "natural" the biological complex, the better will be the balance and the greater the number and variety of pest enemies to cope with an outbreak. This implies, in brief, non-interference with many types of so-called vermin. The encouragement of birds by non-interference and by more positive methods may be noted here. Sylvicultural considerations will be dealt with below.

Artificial Controls in Place of Pest Enemies are chiefly applicable to small-scale operations for biological and economic reasons.

Dangers and Objections. Large-scale chemical warfare on pests must be criticized seriously on grounds of its non-selectiveness, i.e. it kills indiscriminately, including many beneficial life forms as well as the pest we seek to destroy, and may thus do incalculable damage.

Methods may be summarized as follows:

Traps.

Deterrents.

Insecticides: Caustic or suffocating oil-film sprays, poison sprays—arsenate and other compounds.

Modern insecticides: Pyrethrum and D.D.T. sprays and powders.

It is outside the scope of this paper to enter into control methods in detail: it must suffice, therefore, to mention the main lines of application, as above.

(B) *Shade-lovers.* Typical examples of forest "pests" of this class are to be found among aphids and *Adelges*. These feed for the most part on the shaded, light-starved lower branches, which, owing to their consequent deficient sap condition, have reached optimum condition for such insects. Equivalent conditions of lowered sap content in the entire tree are produced when for any reason it falls into a state of reduced health, and it thus becomes susceptible to attack on all portions, not only the lower dying branches.

Prevention. Correct sylvicultural planning (choice of site or species) and management can or should obviate epidemic occurrences, by maintaining health; prevention being achieved through limitation in this way of the *antecedent* food factor.

Control. There are occasions when ill health, promoting epidemics, can arise through unpreventable causes already mentioned such as fire, drought, etc. In such cases, failing quick removal of breeding material, reduction by enemies or enemy-substitutes, becomes the only alternative left. (It should be noted, however, that the likelihood of most of these unavoidable accidental causes appearing can be reduced to a minimum by a system of group planting in mixture, especially when hardwoods are included in the mixture.) It cannot be too strongly stressed, however, that in a case where the wrong site has been chosen for a tree species, the adverse physical factor or factors will continue to operate to the detriment of the trees' health (insufficient light—cf. alpine larch removed to low elevation out of intense ultra-violet zone).

In other words, the food supply of the pest becomes virtually unlimited, so that reduction, or (even were it possible) removal of such pests through their enemies, will never alter or materially improve the state of health of the trees.

The question of whether destruction of such "pests" through enemies, or by chemical control, is practicable or advisable on a field scale—when this has arisen through a *temporary* lowering of health by physical causes—has not yet been given adequate consideration. It is probable, indeed, that as such trees subsequently recover in health, aphids and/or *Adelges* will disappear with the first unfavourable weather phase according to the periodic change trends.

Control of Soil Pests. These are light-avoiders with comparatively unlimited food. Control must, therefore, be attempted by the increase of enemies or chemical or mechanical substitutes. The latter can be economical in nurseries and often advisable as a quick immediate measure, because of the limited area involved. Birds and insect predators are beneficial on a long-term basis.

Chemical methods are here briefly indicated:

1. *Sterilization by Formaldehyde.* Kills soil pests and improves growth by releasing in a readily available form chemical compounds in soil (chiefly nitrogenous) for plant food. This is also the case with sterilization by steam.

2. *Gammexane* (Fygran) has recently yielded good results with wireworm and leatherjacket pilot tests.

3. *Soil Fumigation.* CS_2 (carbon bisulphide), etc., by soil injector are older standard methods.

In this connection, chafer epidemics follow a periodicity, probably largely influenced by sequence of climatic conditions during an 11-year period or less. Chafer in the north appear to follow the full cycle from recent confirmatory reports received from Darnaway and SW. Scotland.

(C) *Light-avoiders.* As has already been explained, many of these require food in reduced health and, therefore, control of such should be effected by *reduction* of the *antecedent* factor, food. Such control becomes one of careful sylvicultural forethought and planning.

The lines of approach will comprise correct choice of tree species, race, or mixture for a given environment, by ecological study of the area under consideration; and by careful subsequent management, the promotion of maximum health of the trees by correct thinning measures and by removal of sick or suppressed trees.

Excepting such accidental increase of sickly trees as is occasioned by fire, wind-blow, seasonal drought, or frost, pests belonging to this class will have no supply of food on which to become established in dangerous numbers, from which epidemics might arise. The accidental occurrence of breeding material in healthy woods is thus not a serious one, since pests will confine themselves to the already injured material.

If woods have been wisely planted and adequately tended, trees will recover from seasonal drought before epidemic numbers can develop, unless drought should recur for two or more consecutive seasons, when consequences from such "pest" increase may be serious.

The artificial creation of large breeding grounds for this type of insect is purely sylvicultural and will be dealt with in detail in the next section.

(D) *Sylvicultural Causes and Prevention of Forest Epidemics.* In order to come to an understanding of the sylvicultural causes of epidemic outbreaks of insects of this class, it is necessary to follow briefly the biological changes in environment which accompany the progressive stages from natural mixed forest to present-day artificial types of woodland.

In tracing the argument through the different stages of ecological conditions to certain biological conclusions, it should not

be understood to constitute a condemnation of modern sylvicultural systems.

Present-day systems have their advantages, else they would not be so freely indulged in.

What it is intended to show are the biological risks and numerous disadvantages of existing sylvicultural systems in relation to insect pests or epidemics. It is for the forester to decide whether such risks are considerable or negligible, in face of what he stands to gain; and whether he will take the risk or perhaps effect a compromise.

Widespread epidemics of forest insects are comparatively rare in these islands (Britain): when they have occurred I would dare to say that inadequate sylvicultural knowledge or its application has most frequently constituted the *fons et origo mali.*

Consider then, on a comparative basis, the biological conditions obtaining in the different types of woodland from the most primitive (natural) to the most specialized artificial systems.

(*a*) *Natural Woodland.* Natural woodland, mixed or pure, contains all ages and types of tree. Of these, some will be dead, some dying, some old and losing vigour, others suppressed and weakly, while the bulk of the standing crop will contain its proportions of inherently weakly, normally vigorous, and super-vigorous trees. Surveys of a number of natural woodlands, making counts of all classes of material, would provide a standard proportion of these classes in a wood of normal health, for comparison with that found under the various artificial systems for a unit area.

Among the varied insect life concomitant with woodland of any type are saprophytes—pure scavengers which accelerate the decay of dead trees by feeding in and on the dead wood.

Others, essentially, but not completely scavengers, find that dying or sickly trees are sufficiently sapless to meet their food requirements and, by invading them, hasten their death and decay. Both these edaphic types thus confer a benefit on the tree populations which support them, eliminating the weaklings, the diseased, and the decaying, and thus maintaining the normal health standards of the wood.

The proportions of these types of food material in a natural wood will be found to vary little and will always be low, but in modern woods, under present-day sylvicultural systems, the position is greatly altered and with it the above mentioned proportions; these classes of insect food material often become greatly increased and the scavengers and hygiene workers of the insect population rise proportionately in consequence to clean up the increase and restore the health balance. Such artificial methods as planting of pure forest (with unsuitable species, or under ecological conditions

unfavourable to such) in even-aged stands, on an unsuitable site, inevitably increases the proportion of weaklings, sick or diseased individuals; and the insects which attack these should be looked upon as beneficial rather than as pests.

As has already been stated, such insects are subject also to periodic physical influences, producing epidemic tendencies; but it is at once apparent from the previous statements that epidemic occurrence is here wholly conditioned by the amount of suitable food material present.

The Ecological Complex. Natural woodland then consists in most cases, in the more temperate zones and elevations, of a mixture of species, and in every case of a mixture of age classes. Frequently a variety of undershrubs with a consequently varied ground flora is present. Here the forms of life (invertebrate and vertebrate) which such a complex contains are very much greater in number and species than can be found in a regulated even-aged stand of a single species.

It is important at the start to appreciate the following contrasting conditions:

1. For a given area, in a natural state, there exists a vast number of inter-dependent factors; each biological factor containing a *limited* number of individuals.

2. For the same area, when the vegetational factors are reduced by planting pure or even-aged woods, the number of zoological factors become correspondingly very much less. The population numbers of each zoological factor tend in consequence to become proportionately increased. A moment's reflection makes it clear that Condition 1 spells safety, Condition 2 danger.

e.g. The number of pine trees attractive to bark beetles in a natural mixed wood or an uneven-aged pure stand of normal health is limited, and the bark beetle population correspondingly so. On an *equal area* with an even-aged stand of the same pine, the food material suitable for bark beetles is proportionately very much greater and the beetle population consequently much higher.

The biological position may be summed up as follows:

In natural woodland there is a standard proportion of super-vigorous, normally healthy, inherently weak, over-aged, suppressed, dying and dead trees. As an old tree dies, seedlings compete to fill the gap. Weaklings are suppressed and probably become diseased before they die. It is clearly advantageous to the wood as a whole that such undesirable individuals become eliminated as quickly as natural processes allow. This is the function of bark beetles, weevils and other creatures. By feeding and propagating they serve the wood's best interests and are hence essentially among the wood's greatest benefactors. In this large natural complex they do

not, cannot, overstep their bounds, being limited by their biological surroundings, to that small, unhealthy minority of trees which forms their right and proper sphere; while they are at the same time further controlled by the variety of insect, bird, animal and other life which preys upon them, to take no present account of the physical factors exerting the same ultimate control.

(*b*) *Artificial Woods.* (i) *Pure Wood, Uneven-aged.* The first step taken by man towards uniformity, for his own greater convenience, is the removal of species which he does not require. Artificial forestry favours pure woodland of one species (monoculture), or occasionally a mixture of two, rarely more; while in this country at least, hardwoods are at present almost completely ousted by conifers in planted woodlands, and in consequence undershrubs are also absent.

The immediate biological effect of this is to reduce the factors in the complex to a very marked degree. Insectivorous birds are greatly reduced through lack of suitable nesting sites, variety of food, suitable undergrowth, and reduction of ground flora; while predaceous insects are similarly reduced for the same reasons.

The proportion of conifer-feeding insects is at the same time greatly increased in a pure coniferous wood, because of the increase of available food material.

This is, in effect, an increase in timber-breeding insects, with a reduction in the numbers of bird, mammal and insect species which would normally prey upon them.

(ii) *Pure, Even-aged Woods.* For practical convenience in computation, management and extraction, there is little doubt that this present is the easiest system to work.

The attendant biological risks are, however, further increased. A species of tree has, at any given age, insect and other enemies peculiarly associated with that particular age; these enemy species varying with youth, adolescence or maturity of the crop.

The establishment of even-aged stands still further reduces the interacting biological factors in the complex. Suppose the plantation to be ten years old, insects preferring their host tree at this age congregate on the area; if the wood be mature, other insect species increase similarly. In each case their food material is proportionately more abundant than in the uneven-aged wood, while access from tree to tree has no obstacles or barriers.

With each step towards uniformity an inevitable increase is being stimulated, through increased food material, in a specialized insect population, since the *proportion* of weakly and suppressed trees in an even-aged stand on a given area is necessarily greater than obtains with an uneven-aged or a mixed wood of equal area.

So long as normal health can be maintained in the plantations,

this increased beetle population may still be essentially beneficial in maintaining the health of the stand by more rapidly eliminating the undesirable proportion of the crop.

The risks and drawbacks consequent on this reduction of associated predaceous and parasitic pest-enemy species through progressive stages of monoculture, along with the inevitable build-up in population of species such as bark beetles and others potentially harmful to the crop, may be summarized as follows. Potential dangers consist of large food units in pure conifer stands which maintain a large skeleton population of beetles which will quickly increase to take advantage of results of seasonal drought, fire or frost, in a manner not possible with mixed woods, mixed age-groups or small age-groups, or species units on the same area.

1. *Clear-felling of Large Pure Stands.* Weevil and/or bark beetle populations, already increased by monoculture, congregate to such an area, to increase enormously by further breeding there. Valuable years are lost in delayed replanting and the soil also deteriorates while waiting for stumps and waste wood to dry out sufficiently to be no longer serviceable as weevil breeding grounds. Money is spent in cumbrous trapping methods to save newly planted crops in this or on adjacent areas from weevil or beetle destruction.

2. *Neglect.* Neglect in maintenance, such as delayed thinnings (how often unavoidable?) results in an abnormal increase in proportion of trees of reduced vigour, which should have been eliminated in thinnings and cleaning. These fall ready victims to the already more than normal weevil and bark beetle populations.

3. *Faulty Sylvicultural Systems.* Clear-felling or over-thinning on an exposed site will often result in wind-blow where large area units are involved. So also may frost damage, sun scorch and local drought. The resultant lowered sap pressure in each instance produces ample suitable food material for beetle and other potential dangers, which are not usually slow in responding. Again, the larger the unit area involved, the greater the damage and risk.

4. *Wrong Choice of Site or Species of Crop.* The immediate prospects of financial gain based on the current state of the market will often prove a temptation to plant an apparently profitable species on sites which are doubtfully suitable, or which are even so utilized without any regard to the elementary physical requirements of that species. Sooner or later the health of the crop suffers, frequently through drought, which induces over-susceptibility to frost. Fungal and insect attack rapidly succeed to these troubles, the lowered sap flow and, therefore, lowered vitality resulting in optimum breeding and feeding conditions for both.

Two examples of this may be cited:

(1) European larch, having a high market price, and as a quick grower producing early returns, has been very widely and indiscriminately planted during recent years as pure wood for the most part. In many instances the sites so employed were quite unsuitable through soil or climatic conditions; often both. The trees in early adolescence showed signs of losing health, frequently owing to direct drought conditions; they then became more susceptible to frost dangers. Either or both of these damaging physical causes were rapidly followed by canker attack, along with epidemic spread of shoot moth; these being succeeded by appearance of *Adelges*, favouring (like canker) the reduced sap condition of the trees, which thus rapidly increased to epidemic proportions.

(2) Sitka spruce was and still is widely planted as pure wood, or in mixture with larch and sometimes other conifers. Where it has been planted on dry *Calluna* sites well within a frost level, it has responded with abnormal needle cast after spring frost (often then attributed to *Neomyzaphis*) [1], to be followed up the succeeding spring by very severe frost damage causing immediate death in many cases. The thus induced low sap-content of injured trees has brought on an attack of *Pityogenes bidentatus*, the only outward sign of health disturbance being needle-cast.

It is noteworthy that in each instance the fault lies in the choice of site; the appearance of the insect being a *result*, not a *cause*, of ill health.

Taking the broad view, these insects are still exercising their normal beneficial function in assisting elimination of sickly trees; but here the proportion of these has increased to the extent of almost the whole area.

(iii) *Complete Uniformity of Crop.* In the continual modern drive towards greater and greater uniformity, sylvicultural practice approaches a critical phase today, attended by very great dangers for the future.

The presence of a normal proportion of suppressed, over-aged or dying trees supports a useful proportion of beneficial scavenger beetle population.

Now, in the determination to attain complete uniformity, all suppressed weakly and dying material is to be removed, and thus, with it, the normal food of this scavenger beetle population.

Not only so, but of even greater importance is the practice affecting the other extreme. "Wolves," so termed (in fact, that proportion of the crop having super-abundant vigour), are to be consistently cut out as they appear. The function of these over-vigorous trees is obviously, by cross-pollination with other less vigorous individuals to maintain continually a proper standard of

(1) Frost-injured needles are liable to *Aphis* attack before they drop.

vitality in the species; so that their systematic elimination must inevitably in a few generations reduce the vigour and resistance of the species. The proportion of "wolves" in a crop is never high, and these should be most carefully preserved to fulfil their important mission.

So, at present we find that at both ends every inducement is being given to attract to the main crop an "acclimatized" race of those insects we wish to avoid, by lowering the specific vitality at one end and by eliminating the insect's normal type of food material (sickly or inherently weakly trees) at the other end.

As mentioned above, it requires little financial persuasion by way of a species monopoly in timber markets to initiate the planting up of large areas under that species, much of it on ground and situations quite unsuited to it; and in this way to lower the health level to a point which invites or demands attack by insects and fungi in precisely the manner demonstrated for the case of European larch and for Sitka spruce; and this particularly when the susceptible state of the tree coincides with a periodic epidemic phase of one or some of the insects concerned.

(iv) *Sylvicultural Prevention of Epidemics.* Biologically, prevention is simple in formula. Progress along the lines of uniformity is progress to trouble. A return to a natural state of woodland, so far as is commensurate with simple and economic extraction and maintenance, will remove the risk of such troubles. Uvarov (1931) cites Graham as finding *Pissodes pini* less injurious in mixed forest where hardwoods were mixed with pine.

A forest area laid out with well planned extraction roads, under a system of group planting, would meet both biological and economic requirements. In such, group units would be of an economic minimum size and could readily be planned to conform to ecological-climatological contour variation.

If specially required, a given group unit could be of one species and even of even-age; but the main point would be realized, namely, that on a whole given area one would have, in effect, a mixed wood of uneven age. With hardwoods and undershrubs included in proportion in such a system, insects such as weevil and bark beetle would not only be diffused over the area, with their population reduced to near-normal proportions, but their access to fresh breeding grounds would be regularly interrupted and impeded by the mixed groups, while the agencies controlling bark beetle, weevil and other potential pests would be increased in species and numbers to something approaching a natural and adequate balance, in birds, mammals and insects. Furthermore, the serious weevil menace to the replanting of large felled areas now obtaining under present methods would be virtually non-existent.

Such a system requires forethought, planning and extra care and labour in maintenance, but, based as it is on biological fact, it would be economically sound.

Monoculture and uniformity are the lazy way, leading inevitably to greater labour, trouble and loss. In order to avoid these, we must revert to natural conditions as far as is practically possible.

V. RESEARCH FIELDS

Introductory. Scope for research is extremely wide, extending far beyond the bounds of biology. The whole subject includes in its orbit astronomy, meteorology, physics, biochemistry, botany and zoology. Obviously it cannot be expected that any worker or body of workers on the biological aspect of periodicities and radiation should also be competent to deal with the related problems where solution is purely physical or meteorological. Thus a mutual agreement would be necessary whereby essential research which was purely physical or meteorological could be referred to the appropriate experts in their own branch of science, the combined results and information being pooled and brought together.

The question of research may be conveniently led up to by a review of ways in which forecasts could be arrived at; the basic information necessary for their composition, and the practical application which such forecasts could have in regard to prevention and control.

(1) *Construction of Forecasts with Prevention and Control Application.* (*a*) *Astronomical.* Further study of sunspot periodicity leading to a full comprehension of what at present appear to be somewhat contradictory discoveries, involving 11-year, multiple, fractional and other cycles, forms the foundation of all forecast work. As all these independently discovered periodicities must form parts (or different aspects) of one general pulsation, however complex, a fuller understanding of this complex, periodic, solar-energy pulsation is necessary, in order to modify or correct and finally integrate these separate periodicities into a coherent whole. This belongs to the sphere of astronomy or astro-physics, and on this all subsequent research regarding meteorological and physical data must be based. Given this, it will then be possible to forecast with some degree of accuracy the periods of sunspot maxima and minima, along with a quantitative measure of the actual sunspot and its resultant radiation increase or decrease, for a considerable period ahead.

Research on these lines is liable to be a long-term work, entailing the accumulation of sufficient records from which to derive the necessary data.

(*b*) *Physical.* Quantitative measurement of ultra-violet, light and other radiation intensity for the different maximum and minimum

points throughout all the fluctuations of the complete sunspot cycle are a matter falling into the realm of pure physics. Another essential collection of data would be the measurement of ultra-violet, light and other radiations (normal or average) within a series of elevational zones over sufficiently representative geographical climatic regions. The measurement of solar radiation forms a necessary prerequisite to the forecasting of epidemics, construction of zoological and botanical climographs (or "radio-climographs"), as well as forming a definite ground on which weather trends may be correlated with periodicities.

The measurement of radiation intensities, particularly infra-red, light and ultra-violet over a series of elevational zones (to be determined by ecological study) is essential to a determination of the optimum radiation conditions in the ecological environment of certain plants and plant associations, with their dependent insect, bird and animal populations. On this basis, combined with the above mentioned solar radiation measurement, it will be possible to assess optimum radiation figures in general and detail for important tree and plant crops and for any potentially epidemic-subject insect and other examples, for any ecological climax. Thus, with the aid of radio-climographs, we can predetermine with more complete accuracy than heretofore the advisability of introducing a new species of plant or animal into new ecological surroundings—its chances of maintaining health or of becoming susceptible to pests or disease.

The measurement of the ultra-violet optimum for a potentially epidemic species can now be compared with a graphical representation of general ultra-violet fluctuations through a complete cycle and thus its potential epidemic periodicity found. Hence the years of potential epidemic outbreak can be forecasted, whether regular or not in recurrence, after combining these data with local or general study of weather trends, to compare with optimum temperature and humidity conditions.

On these general lines, forecasting of epidemics may one day be developed to a fairly exact science.

A secondary physical problem exists in the chemical composition of "snow water." Water from melted snow contains an extra hydrogen ion. Snow is more abundant at high elevations where ultra-violet is strongest. What connection may there be between the greater metabolic stimulus to alpine plants in spring when snow melts and water is abundant, with the extra hydrogen ion in the latter? Are the two facts complementary, enabling the plant to assimilate and build up more food material for a given unit of water taken up as compared with conditions at low elevation with less ultra-violet

stimulus and the extra hydrogen ion lacking in the water supply, bearing in mind also that many alpines flower in spring?

(*c*) *Meteorological.* Much work has already been done to correlate weather and climatic trends with sunspot periodicities, as for example, the already cited simple 11-year cycle, with hot and dry conditions during minima, warm and humid approaching and during maxima, and cool, dry seasons between maximum and minimum intensities. Further confirmation of the degree of exactitude of these weather correlations is necessary. Then, only when the complexities of the sunspot periodicities have been clarified and fully comprehended, will it be possible to approach a long-term forecast of weather conditions based on sunspot periods.

The value of being able to forecast seasons of drought or high rainfall, heat or cold, is at once apparent for farming, horticulture and forestry. (This has been successfully carried out in U.S.A. in connection with droughts and flooding.) In addition, though ultra-violet may provide the stimulus, without the necessary climatic conditions of heat and/or humidity, epidemics and swarming will not take place with certain species; indeed the increased stimulus without the optimum atmospheric conditions and seasonal climate are more likely to prove injurious to a potential epidemic of certain species.

At present, a forecasting of broad general climatic trends has been shown to be possible over sunspot periods and that for possibly an indefinite number of years. But to be of biological value, further study in order to make accurate, local short-term forecasts of weather, say, not more than two seasons ahead, is necessary.

These more immediate local forecasts would decide whether a potential epidemic was likely to develop, and thus whether to give warning to take precautions in advance.

Detailed knowledge of climate, i.e. average monthly temperature and humidity, are essential to the compilation of climographs. The making of "radio-climographs," i.e. the plotting of monthly figures for ultra-violet intensity as against monthly humidity or precipitation for two sites a considerable distance apart, would give invaluable information regarding the comparability of conditions in the native district of a species and the proposed new district of introduction. For this, climatic forecasts would be of value, ensuring avoidance of the least favourable climatic phase in the periodic cycle, when effecting the introduction.

(*d*) *Botanical.* Record of plants associated with each of a complete series of elevational contour zones, where a light and ultra-violet intensity value has been obtained for each zone, will give an index of the optimum ultra-violet and light tolerance of the different species. Study of local variations may be necessary where aspect,

etc., alters radiation conditions appreciably, also where plants grow in shady conditions, under trees, etc. Naturally, cultivated plants, such as trees, agricultural and horticultural crops, would come under consideration first. With the data obtained, providing a measure of radiation intensity over a complete 11-year cycle in the first instance, along with a knowledge of the atmospheric conditions obtaining at such times, a much more exact index will be found of the optimum ecological environment of any species. Study at the same time of plant responses to infra-red are equally essential. For quick reference, all this information could be expressed in radio-climograph form.

Forecasting from these data can be simply and quickly made. Firstly, as previously stated, it can be immediately forecasted whether introduction of a species to a new environment will meet with success, by radio-climographic comparison before planting, of native and the new surroundings. This would save many mistakes involving much labour and expense, both in the actual planting and in the subsequent attempts to counteract sickness and disease symptoms as they appeared.

Secondly, comparison of the plant's radiation optimum with the optimum intensity promoting epidemics of such pests as it is liable to, along with the radiation intensity of any given locality in which it is growing, if this varies from the plant optimum, will enable accurate forecast to be made as to whether and when a pest epidemic is likely to attack this host plant: (1) Where radiation conditions which will stimulate pest epidemics are also optimum for the plant, and (2) where these are above or below optimum for the plant.

In either case when such were practicable, preventive or control measures could be prepared in advance. Use would be made of more immediate weather forecasts covering the current seasons in the forming of such immediate forecasts.

The following example should serve to clarify this.

A plant introduced to a different physical environment finds the new ultra-violet intensity far below its optimum. This ultra-violet intensity is, at the same time, the optimum for indigenous insect and other fauna, as well as fungi, which are liable to attack it. If such insects and/or fungi require a state of reduced vigour or a degree of ill health on the part of their host plant, there is a strong likelihood that, given the optimum climatic phase, they will increase rapidly to epidemic proportions to the serious injury, if not destruction of the crop.

Where ultra-violet and radiation and atmospheric conditions in the new environment are substantially the same as in the plant's native environment, attack by pest epidemic will, in the first place, be quite unconnected with the introduction of the plant to its new

environment; in the second place, the plant, being in full vigour and health, will suffer less from attack, which also will be limited to insects whose epidemic increase is controlled entirely by ultra-violet periodic fluctuation, and not, as in the previous case, in any way dependent on a pathological condition in their host plant.

The following corollary would then appear to evolve out of this:

Where ultra-violet (or radiation) optimum is similar for host plant and pest, the likelihood of serious damage to the host plant is less. Where radiation is at an optimum for pest and not for host plant, the likelihood of damage to the host plant and inevitability of pest epidemic occurrence become greatly increased. Correlation of full seed years in trees and other such occurrences which take place periodically at multi-annual intervals, with sunspot cycles, requires more detailed study. For each species a sufficient number of records must be collected, so that the particular phase of the sunspot cycle during which it occurs may be indicated more exactly. This can be further checked by precise radiation or ultra-violet intensity measurement. From these data forecasts of such occurrences could be made with reasonable certainty.

(*e*) *Biological.* The data needed for the making of forecasts in the biological field are necessarily in many ways similar and redundant to those required in the botanical field. The problem here is, however, a more direct one, being chiefly concerned with the physical stimuli, on the one hand, and epidemic response over a periodic cycle, on the other.

Insects (and other species among mammals, birds, etc.) which are subject to epidemic increase could be first of all graded according to the normal light conditions of their environment, as has been done on Section III, as follows: (A) Full Light-tolerant, (B) Light-tolerant, (*a*) Shade-dwellers, (*b*) Light-avoiders, (i) Root-feeders, (ii) Food-burrowers. Collection of past and future records of the phase of the sunspot cycle during which epidemics of each are at their height, combined with actual measurement of ultra-violet (and other radiation) intensity at the height of these epidemics, would

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Diagram 4 *on opposite page.*

CLIMOGRAPH OF TWO SITES

Indigenous = ———— New district = – – – – – – –

Overlapping of two figures, particularly during spring-early summer, shows if introduction of species to new district will be successful.

Substitution of U.V. intensity for temperature in climograph provides more valuable data even than plotting sunshine hours against humidity.

Use of these could probably be of value with pest and host plant conditions when latter was introduced, for forecasting liability to attack. When U.V. intensity for proposed district of introduction was greatly above or below indigenous optimum, the little or no overlapping of the two figures would indicate probable failure of species if introduced.

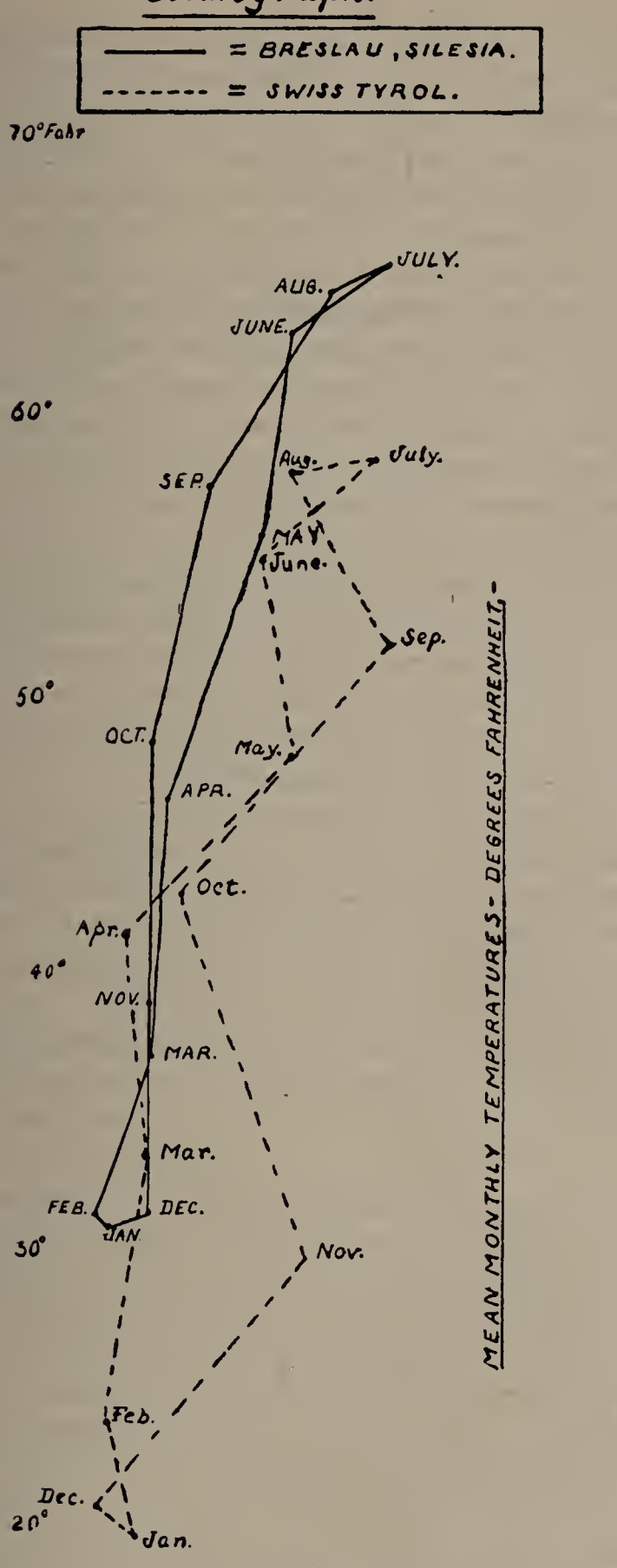

Climograph.
——— = BRESLAU, SILESIA.
------- = SWISS TYROL.
70°Fahr
JULY.
AUG.
JUNE.
60°
SEP.
Aug.
July.
MAY
June.
Sep.
50°
OCT.
May.
APR.
Oct.
Apr.
40°
NOV.
MAR.
Mar.
FEB.
DEC.
JAN.
30°
Nov.
Feb.
Dec.
20°
Jan.
15°Fahr
MEAN MONTHLY TEMPERATURES - DEGREES FAHRENHEIT -
1" 2" 3" 4"
MEAN MONTHLY RAINFALL - INCHES -

DIAGRAM 4

establish with fair exactitude the precise phase relationship of epidemic appearance of a species with the sunspot cycle.

From such figures, it would be comparatively simple to identify the points on a graphical representation of the full sunspot cyclic system; which species coincided with these figures; and hence to forecast epidemic probability over a period of years. Subsequent comparison of optimum climatic conditions with more immediate weather forecasts would make accurate close-range forecasts possible. It has already been noted in Section III how such forecasts can only be made with any certainty for species whose epidemic occurrence is not conditioned by a pathological development in their food plant; i.e. definite forecasts must be confined to those insects directly affected by ultra-violet and light stimulus. Forecasts coming into the probability range may be made for the others, where, obviously, epidemics can only arise when there is sufficient food supply.

The value of such forecasts in the advance planning of deterrent, preventive or destructive measures against pests, is at once apparent. The breeding and release of predators and parasites could be accurately timed with a much greater degree of certainty than is at present possible, to ensure maximum results.

On these lines, then, the forecasting of epidemic recurrence of insect, mammal and bird plagues could be reduced to an exact science. The wisdom of introducing a species of plant or animal could be assessed beforehand with certainty.

Release of predators or parasites to combat an epidemic could be timed to obtain maximum results.

The benefits of these forecasting practices to agriculturalist, horticulturist and forester are at present almost incalculable.

II. Control by Radiation.

(A) *Outline of Future Possibilities.* The fundamental facts from which control by radiation must be developed centre around the phase relationship of insect and other epidemics to the radiation accompanying sunspot maxima. To date, biological interest has been chiefly focused on response to ultra-violet increase over such periods. Measurement of this ultra-violet radiation at peak intensities and at optimum intensity for such insects as we are concerned with have already been recommended in the discussion on forecasts. Such measurements are essential to planning of schemes of control by radiation, not only for ultra-violet but also for the various colour-zones of the light spectrum, where optimum radiation conditions are likely to lie for certain species and also for the infra-red spectrum.

For as it is now apparent that an insect has an optimum intensity at some point in the radiation spectrum, so also it must have an adverse maximum intensity, beyond which life ceases to be possible.

Between optimum and pessimum lies a toxic zone increasing in effect up to the adverse maximum or lethal point. Below optimum to a certain minimum intensity lies a zone within which conditions favour normal health and vitality, while below this degree again lies a low intensity ultra-violet zone which is too low for the maintenance of health of the species.

Reference to the accompanying diagram will make these points clear, while it is apparent that experimental work alone will fix these various points for a given species. (Diagram 5).

This has been in consideration of radiation *intensity* for ultra-violet only, for a species positively responsive to this radiation. Obviously, the principle has similar potential application for other radiations to which a species shows positive response. Thus to a species showing a positive response to infra-red, a similar intensity graph can be constructed, and possibly similarly for the light spectrum in whole or in its component parts.

Experiments made in U.S.A. and cited in Section 1, of exposing beetle-infested logs to radiant heat, are in line with this suggestion.

Another aspect arises out of this. If a species is positively responsive to ultra-violet, is it therefore negatively so to infra-red? The answer to this may be yes, though not necessarily so, in all cases. Where response is found to be negative, we have an indication here also of a possible line of control, arising not out of change of *intensity* of a particular radiation, but change of *wave-length* in the spectrum.

In a natural environment, of course, it is not possible to say, as the accompanying wave-length zone figure would suggest, that optimum conditions lie in, say, the blue-violet wave-lengths; since the insect in its habitat is perforce exposed to radiations extending through the whole terrestrial spectrum inclusive of some infra-red, all light and some ultra-violet.

But experiments to date made with rearing or keeping insects, continually subject to certain wave-lengths only, to the exclusion of others, show that they respond most favourably to certain wave-lengths, and unfavourably to others. Experiments on these lines have been made chiefly in the colour spectrum and in ultra-violet, while a little has been done with infra-red; these having already been referred to in Section I. (Diagram 6).

The two lines of control arising out of these considerations may be stated as follows:

1. If an insect shows optimum response to a particular wave-length *intensity*, can increase or decrease of that intensity to a certain degree prove fatal?

2. If an insect shows optimum response to a particular *wave-length*, can exposure to one of sufficiently different frequency prove fatal? e.g. Can a pest be killed by exposure to infra-red whose

response to ultra-violet is positive, and vice versa? Results of experiments made to date suggest that this may prove to be a potentially productive field for experimental control.

The line of research to follow up would tentatively appear to be somewhat as follows:

1. (1) Find the optimum wave-length and intensity for an insect pest (under controlled and carefully recorded temperature and humidity conditions).

(2) Find the pessimum wave-length for this species.

(3) Increase intensity of pessimum wave-length, finding at same time most effective coincident temperature and humidity conditions, to a point which secures fatal results at minimum intensity increase. (Minimum intensity is desirable primarily in respect of potential injury to host plant or immediate environment.)

(4) Repeat these experimental findings on host plant or environment (where latter is stored food such as flour, grain, dried fruit, etc.) under same temperature and humidity controls to find non-injurious intensity limit.

2. Find optimum intensity of ultra-violet for positively responsive species, increase intensity to fatal toxic point. Similarly with infra-red.

Different intensities of these may also be employed on insects irrespective of positive or negative responses.

Maintain humidity and temperature controls, with recordings and observations.

We know, of course, that ultra-violet of sufficiently high frequency will kill. But the former line appears more desirable as being less injurious to pest environment and the radiation may be less expensive to produce artificially. For certain pests, radiation of high penetration will be essential and therefore experiments with infra-red may give useful results.

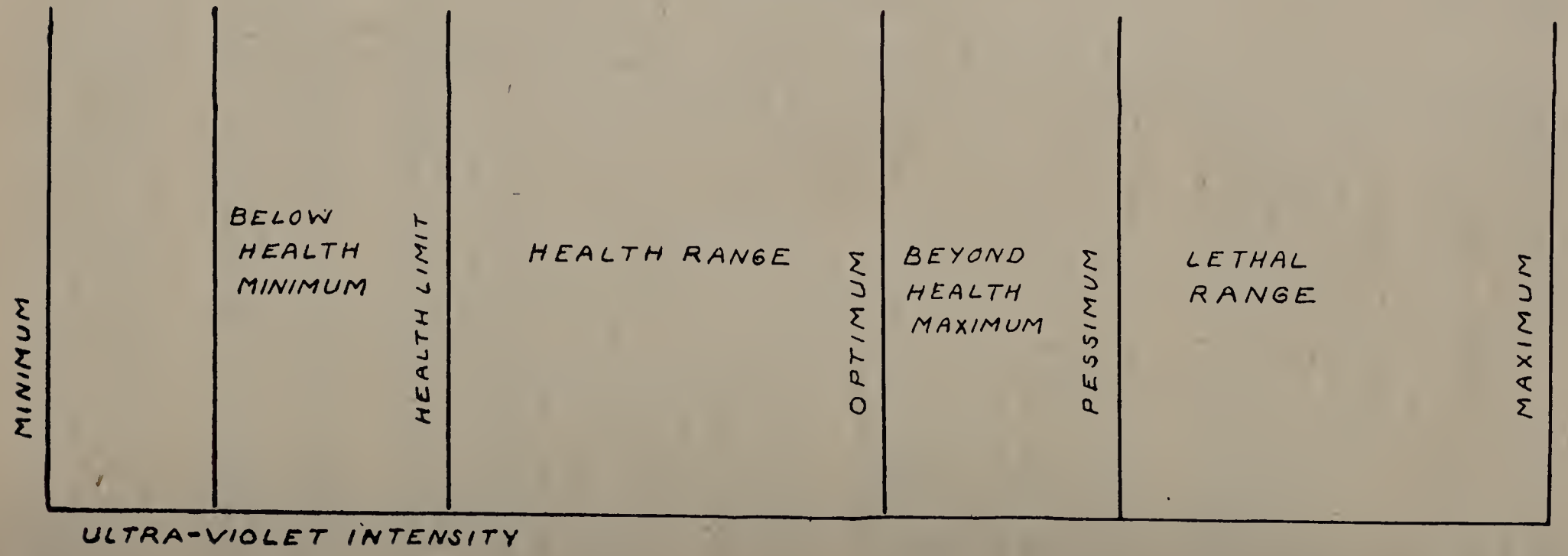
(B) *General Application of Control Principles.* In previous sections, insect types have been grouped according to their light or radiation environment, and it will be convenient here to run briefly through these groups with a view to possibilities regarding this type of control.

1. The most light-tolerant types react favourably to intense light and to ultra-violet.

(Why do night-flying moths, which avoid daylight radiation, exhibit such a strong attraction to artificial light and ultra-violet after dark? Is it confusion of light radiation with some other invisible sexual stimulus?)

Certain of these showed quicker larval development under ultra-violet, violet and blue wave-lengths. Experimental work on such would take the form of increasing intensity or frequency of ultra-

DIAGRAM 5



Hypothetical representation of optimum ultra-violet intensity for a species, showing health range, ill-health and lethal ranges.

violet (from a known optimum for preference) and also of exposure to infra-red, at frequencies or intensities innocuous to host plant, etc. Over-stimulation by ultra-violet may be found to have a sterilizing effect on reproduction, or an atrophying effect on reproductive development.

2. Shade-lovers, whose optimum wave-length lies somewhere in the colour spectrum, will probably show unfavourable reaction to lower ultra-violet frequencies than do the last group; while their reaction to increasing intensities of infra-red may yield valuable results.

3. With light-avoiders, which have been shown by experiments in the past to react unfavourably to ultra-violet and blue, purple or strong white light, or to react favourably (at least, positively) to infra-red, their exposure to penetrative high-frequency radiation or to increased infra-red intensity may prove toxic, particularly under certain humidity conditions. Those insects which showed epidemic increase during sunspot minima with hot dry weather conditions might be expected to react fatally to exposure to a combination of high-frequency radiation, high humidity and/or low temperature.

Application. Mobile apparatus for treatment of sub-surface pests, in trees (just under bark), in surface soil on limited areas, has a potential future for bark beetle, wireworm, cutworm and leather-jacket control, by penetrative radiation.

Penetrative radiation such as infra-red at sufficient intensity, or simple radiant heat effect by exposure to strong sunlight as already effectively employed in U.S.A., has a definite scope for further development in the case of felled (unbarked) logs infested with bark beetle, seasoned wood, stored food products and seed supplies. Treatment would be simplified in many cases where it could be given in enclosed space such as timber yards and warehouses. Similar ultra-violet treatment may also show beneficial results in the case of aerial stages of stored-food pests of low frequency optima (e.g. *Borkhausenia*).

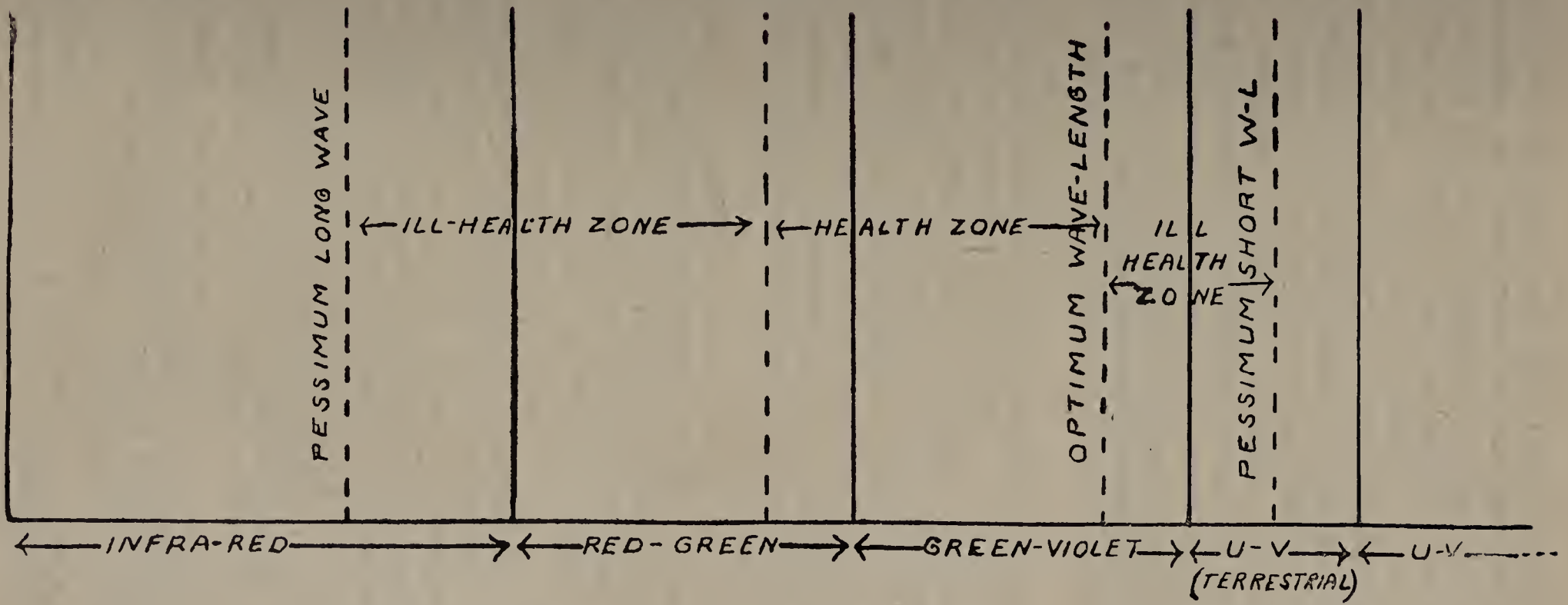
Greenhouses and nursery beds are fields which may yield good results from trials with mobile ultra-violet and infra-red equipment.

In all cases careful tests would have to be made of the effect of any effective exposures on plants, timber, wood, stored foods and seeds, while coincident temperature and humidities would have to be carefully controlled and recorded throughout.

III. Suggested Lines for Biological Experiment.

Introductory. Much of what belongs to this section has already unavoidably been touched on in the previous section on radiation control. There are still questions and problems, however, distinct

DIAGRAM 6



Hypothetical representation of optimum point in spectrum for a species, showing ill-health zones, health zone and pessimum toxic zones above and below optimum.

from control, which need solution, clarification and confirmation, which it will be well, in conclusion, to draw attention to.

(A) *Botanical.* Plants (and animals) "absorb" radiant energy from different parts of the solar spectrum. Colour variation in plants, both leaves and flowers, is linked up with this. Certain work has been carried out in this connection, but much precise knowledge has still to be gained regarding the exact physiological response of plant organisms to the different wave-lengths. It is known, for instance, that ultra-violet stimulates anabolism; infra-red, metabolism, catabolism and hormone production. Ultra-violet and white light inhibit growth. There still remains much to be found out with regard to the more specific stimulus of each defined area in the spectrum. For instance, does each colour band in the light spectrum induce a different physiological response in the plant? If so, what are they?

Flower-colour is another field. Predominance of purple, blue and white with alpines, where ultra-violet is more intense; predominance of yellow and white early in the season, with succession of red to blue and purple; predominance of red in many damp environments, especially in acid peat and also in dry, would repay further research. It becomes increasingly apparent that many of the plant's physiological and morphological adaptations are less primarily xerophytic and climatic than protections against excessive radiation effects.

There seems no doubt that fluctuations of a periodic nature in solar radiation are largely responsible for periodic flowering, full seed years, and other symptoms of stimulus to fertility and reproduction; but exactly which region of the spectrum promotes this stimulus is not always certain. It may be more than one region which is responsible.

Graham (St. Andrew's Univ.) has conducted much research enquiry into the influence of infra-red on plant physiology; and much still remains to be discovered regarding details of plant reactions in growth, respiration and associated activities.

The determination of radiation conditions in different elevational zones for respective plant associations in each zone has already been discussed (Part V, Section I) along with the benefits such knowledge would confer in the selection of suitable environmental conditions for introduction of new species.

(B) *Entomological.* Confirmatory research is desirable into the details of the connection between radiation stimulus to the nervous system of insects and behaviour, development to maturity, fertility and reproduction, swarming and migration.

Most of the other proposed lines of research have already been touched on or discussed.

Epidemic. Insects which are liable to epidemic outbreaks should be made the subject of a connected series of experiments.

1. Based on their known environment, they may be first grouped according to the headings given in Section III for degree of light tolerance.

Employing immature feeding and (when still feeding destructively on plants, etc.) adult feeding stages in each instance, by subjecting them to different radiations in turn and noting reaction; the optimum radiation can be determined, and, at the same time the optimum intensity of that particular wave-length.

With information a much more precise grouping would be obtained than the above mentioned rather tentative one drawn up in Part IV, and would provide conclusive proof, confirmatory or otherwise, of the deductive conclusions arrived at in that Part regarding degree of light tolerance.

This new arrangement could be grouped in the following manner:

(1) Optimum radiation—ultra-violet.
(2) Optimum radiation—light, specifying colour region in spectrum.
(3) Optimum radiation—infra-red.

Similar information should be obtained for host plants (known and potential, where the latter is of practical value), since knowledge of the degree of similarity in radiation requirement of pest and host would be extremely valuable. From such information the likelihood of epidemic outbreak could be further worked out by comparative study of the optima for plant and pest and of the radiation conditions obtaining on an actual site. The plant grouping on this radiation measurement basis would, as stated elsewhere, enable choice to be made of the best elevational zone, or other site fulfilling demands for crop or tree planting and for nursery sites in the latter case.

2. Following on from this, experiments on their responses to unfavourable radiation conditions would be made easier, and would lead up to the radiation control experiments discussed in Section II of the present part in connection with prevention and control of pests, and in the correcting of choice of site for host plant.

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